TAXONOMIC STUDIES ON *GYRAULUS* (GASTROPODA: PLANORBIDAE)[1]

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ABSTRACT

From 94 mostly Eurasiatic samples, alcohol material of *Gyraulus* snails was compared con-
chologically and 492 specimens were dissected for anatomical characteristics. Infraspecific
shell variation is shown to depend on, among other things, water movement. *G. albus* (Müller)
becomes larger in lenitic biotopes than animals with equal whorl numbers in lotic biotopes. In
animals killed by immersion in ethanol particularly the length of the penis sheath is shorter
than in snails relaxed with pentobarbital.

Characters highly valued for species discrimination are among others: the distribution of
pigment cells on the mantle to the right of the kidney; the presence or absence of distinct
transverse septa in the tubular portion of the kidney, rendering its margins "undulate" or
"straight," respectively; the number of prostate diverticula and their shape and arrangement
in the gland; the width of the vas deferens; the length ratio penis sheath : preputium; the shape
of the penis tip and stylet, and the position of the penis pore. In certain groups peculiarities
occur in various other organs (radula, seminal vesicle, bursa copulatrix, bursa duct, etc.).

Europe harbours five indigenous species of the genus plus six endemic species in Macedo-
nian ancient lakes. North Asia is inhabited by *Gyraulus acronicus* (Férussac) only, while south
Asia harbours a "Rassenkreis," i.e. *G. chinensis* (Dunker) (commonly used junior synonyms:
G. convexiusculus (Hutton), *G. spirillus* (Gould)) with at least eight peripheral isolates. Two new
species are described, i.e. *G. eugyne* from Inner Mongolia and *G. malayensis* from Malaya,
also occurring in Java and Bali. Abandonment of planispiral growth and formation of several
angles or keels on the shell periphery in *Gyraulus* of the ancient lakes is certainly due to
convergent evolution. There is strong evidence from anatomy that a species endemic to Lake
Biwa in Japan has a history different from that in a group endemic to the Macedonian Lakes
Ohrid and Prespa. Two keys are presented: one for identification of the species living in Eu-
rope, the second a provisional one for the west, south, and east Asiatic species.

Analysis of relationships according to Hennig's "consequent phylogenetic systematics" re-
vealed the existence of seven subgenera, i.e. *Torquis* Dall (Nearctic and west Palaearctic),
Lamorbis Starobogatov (west Palaearctic), *Armiger* Hartmann (Holarctic), *Caillaudia* Bourguig-
nat (Ethiopic), *Choanomphalodes* Lindholm (Lake Biwa, Japan), *Carinogyraulus* Polinski (Lakes
Ohrid and Prespa, Macedonia), and a provisional "subgenus *Gyraulus* s. str. Charpentier"
(cosmopolitan except South America and the Ethiopic region). *Gyraulus* s. str., being a remnant
group merely characterized by symplesiomorphies and autapomorphies, cannot be established
as a monophyletic taxon. According to Hennig its paraphyletic character is not excluded. Hen-
nig's arguments appear to leave such remnant groups as a general problem of his systematics.
In the case of "*Gyraulus* s. str." only chorological implications can help to support monophy-
letic status in Hennig's sense. Incompatibility is shown between Hennig's "deviation rule" and
biological reality in the case of the "Rassenkreis" of *G. chinensis*, which is considered to be
the "persisting stem species" of the marginal species that have evolved as peripheral isolates.

The centre of origin and the primary centre of differentiation is probably the west Palaearctic
to which all the genera closely related to *Gyraulus* are confined. A secondary centre of differ-
entiation is the Nearctic, a third one the Indo-Malayan region. A redescription of the genus
Gyraulus Charpentier, 1837, is given using present knowledge on variation of anatomical and
conchological characters.

INTRODUCTION

As in other molluscan groups, diversity of
shell characters has led to excessive naming
of "species" in the planorbid genus *Gyraulus*
Charpentier, 1837. For the South African re-
gion, Brown & van Eeden (1969) have pub-
lished an outstanding revision of *Gyraulus*

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species; the species endemic to Lake Ohrid (SE Europe) have been revised by Hubendick & Radoman (1959); three species of central Europe have been compared anatomically by Meier-Brook (1964). A synoptic view of Eurasiatic forms was, however, still lacking, although repeatedly called for, particularly by those interested in medical malacology (Burch & Natarajan, 1965; Pace, 1973).

The health impact of *Gyraulus* is their rôle as intermediate hosts of the intestinal flukes *Echinostoma ilocanum* Odhner, 1911 and *E. lindoense* (Sandground & Bonne, 1940), which are pathogenic to *inter alia* man.

The number of names created for Eurasiatic species or subspecies of the genus, or later assigned to it, is not far from 200, and only recently three new species have been described from Thailand (Brandt, 1974).

The goal of the present investigation was to find out to what extent conchological variation is paralleled by anatomical variation. Consequently the studies had to be confined to instances where living or preserved animals were available. A revision of North American forms must be postponed since the huge American collections would require years of study. Moreover, American species have so far not been incriminated as hosts of human helminths. In South America there is only one species of this genus (Paraense, personal communication) and the Australian region will be covered by studies now being undertaken by Dr. D. S. Brown. It would be premature to expect a complete revision and list of synonyms, but I hope that the present study will serve as a basis for a revision where results of further studies can find their appropriate places. Great gaps in knowledge remain from central Asia, viz. Siberia and the Peoples Republic of China, where I could collect some material but was prevented from taking it out of the country.

Material to be studied and compared was selected according to the following criteria: planorbid snails with a hollow stylet on their penis and having a shell with three to four and a half (at most five) rapidly increasing whorls. These features have been accepted as characteristic of the genus *Gyraulus* by all authors who have used this name (Baker, 1945; Hubendick, 1955, etc.).

MATERIALS AND METHODS

Snails were collected alive by various persons at the localities indicated in the text un-

der "Material." The animals were usually sent alive and prepared for study at the laboratory of the Institute of Tropical Medicine of Tübingen University; in some cases animals were relaxed, fixed and preserved by the collectors, as indicated in the text. Where freshly collected material was not available, i.e. from the U.S.S.R. and the Peoples Republic of China, I had to rely on old museum collections.

Unless stated otherwise, living snails were prepared as follows: They were relaxed in a freshly prepared suspension of 5 mg or more pentobarbital in 10 ml of tap water at room temperature, as described by Meier-Brook (1976a). After 6 to 12 hr they were killed and fixed in 4% formalin at appr. 60°C and transferred to 70% ethanol until dissection. This was done under a Wild Zoom Stereomicroscope M7 using pointed forceps, microscissors after Vannas, ophthalmologic scissors, and insect needles of the sizes 0 to 000. Camera lucida drawings were done with a Wild drawing tube. Whole mounts of organs and organ sytems were made on microscope slides in Eukitt. For histological studies organs were removed from the body, dehydrated in a series of graded ethanol, soaked with methyl benzoate (2 × 15 min), benzolum (30 min), benzolum/histoplast-S (56–57°C, Serva) (30 min) and embedded in histoplast-S after 8 hr. Serial sections 7 μm thick were made with a Leitz-microtome and stained in haemalum and azophloxine. When organs were too small for exact orientation during embedding, they were stained in an alcoholic solution of safranin prior to dehydration.

Chromosome Counts.—For determination of chromosome numbers, ovotestes and embryos were used in some cases when living snails were available. Ovotestes were excised in tap water where they remained for 15 to 30 min to make cells swell and thus make better chromosome spreads. Embryos were freed from their egg capsules and treated in the same way.

For fixation, tissues were transferred to a mixture of acetic acid and 96% ethanol, 1:3 parts by volume (according to Patterson, 1971). After 5 min they were stained in a concentrated acetic orcein solution for up to 8 hr and differentiated in 45% acetic acid. Preparations were examined in 45% acetic acid after squashing tissues in a screw clamp. Counts were made under a Zeiss interference microscope at 1200×.

SEM-Studies.—Snails were relaxed in a suspension of pentobarbital for 1 hr, fixed at

room temperature in a 2% glutaraldehyde solution, in which the body cavity was opened immediately after immersion. For studies of the penis tip, the penis sheath was cut and the penis drawn out. The organs were fixed for 2–4 days, rinsed in distilled water for 4 × 5 min, dehydrated in 30, 50, 70, 90 and 100% acetone for 10 min each and dried in an ISI critical point drying (CPD) apparatus over carbon dioxide. Critical point drying was performed in the Cytological Laboratory of the Institute of Tropical Medicine, Tübingen, by Dr. H. M. Seitz. SEM studies were performed with a Cambridge Stereoscan Microscope MK2A after coating with C + Pd/Au.

CHARACTERS USED IN GYRAULUS TAXONOMY

The biological species concept (Scudder, 1974) is advocated in taxonomical revisions at the infrageneric level. It is subject to a minimum of controversies aside from dealing with fossils and problems stemming from uniparental reproduction. As every taxonomist knows, however, very few species would be accepted at all if biologists relied on only this species concept. In planorbid gastropods, the fact that all members can self-fertilize poses severe problems from crossing experiments. Only in a few cases does a genetic marker, e.g. recessive albinism, enable one to distinguish between the results of self- and cross-fertilization (Richards, 1973b). In most groups, such as *Gyraulus,* albinotic individuals have not yet been found.

The biological species, however, is not defined only as "the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals that share in a common gene pool" (Dobzhansky, 1950); "the essence of the biological species concept is discontinuity due to reproductive isolation" (Mayr, 1974a: 379). Evidence of reproductive isolation between sympatric populations serves to indicate that different species are involved even if other types of data are unavailable.

Examples of reproductive isolation between species of *Gyraulus* hitherto characterized as morphological species are regularly encountered in Europe. In seven of the nine localities where I collected *G. laevis* (Alder), it lived together with *G. albus* (Müller), and not only in the same water body, but in the same square meter. In all of the eight central European lakes where I found *G. acronicus*

(Férussac) this species coexisted with *G. albus. G. riparius* (Westerlund), too, was found associated with *G. albus,* and the only European species regularly living alone is the decidedly stenoekous *G. rossmaessleri* (Auerswald) confined to temporary pools. Wherever sympatric species of the genus were examined I never saw intermediate anatomical traits indicating hybridization. Doubts arose when only shell characters were considered. But even if hybrids occurred and these were fertile, this would not necessarily affect our statement on reproductive isolation. "What matters is not whether hybrids can be obtained but whether the Mendelian populations do or do not exchange genes, and if they do whether at a rate which destroys the adaptive equilibrium of the population concerned" (Dobzhansky, 1950: 415 *et seq.*).

Sympatry of pairs of European species of course should not be taken as evidence for sympatric speciation. On the contrary, in the pairs *Gyraulus albus-laevis* and *G. albus-riparius* relationships appear remote enough to regard them as members of different subgenera. Although we are far from recognizing the mechanism of reproductive isolation between them, differences in form and size of the male copulatory organs, as shown later, make copulation unimaginable. This is also the case in the pair *G. albus-acronicus* where differences in size (Tables 1 and 2) though not in general morphology are pronounced. There is no reason to assume that events leading to separate species and subsequently to separate subgenera did not occur in geographical isolation. Allopatric speciation with a later reunion of geographic ranges may be the rule in cases where closely related species coexist, although the possibility of sympatric speciation, for example by disruptive selection (Mayr, 1963: 156; Sperlich, 1973: 52–53, 155), can no longer be denied (Scudder, 1974).

A different situation will be shown for a pair of jointly occurring species that have virtually no anatomical differences: *Gyraulus chinensis* (Dunker)-*tokyoensis* (Mori). Here evidence of reproductive isolation favours the decision for separate species.

In the majority of samples from allopatric populations comparison and evaluation of morphological characters, supported by biological and ecological observations, remain the only practical methods for species discrimination. This approach is considered justifiable as long as the following, expressed by Mayr (1974a: 381), is kept in mind: "Repro-
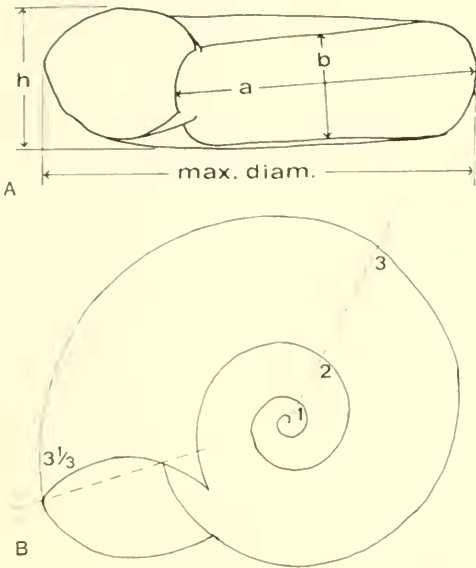
FIG. 1. Dimensions measured (A) and method of counting whorls (B) in *Gyraulus*. Example: *G. laevis*, Kuehren and Ansbach.

morphological species concept since reproductive isolation always remains the primary criterion and degree of morphological difference only a secondary indicator, which will be set aside whenever it comes in conflict with the biological evidence.''

Morphological characters are subject to variation for various reasons: allometric and seasonally different growth, preparation-dependent changes, and, of course, genotypically- and ecophenotypically-determined ones. Although the latter two reasons cannot be separated in a morphological analysis, I later include several paragraphs titled ''Non-Genetic Variation,'' where undoubted cases of externally induced aberrations are dealt with. However, the inclusion of such paragraphs does not imply that the preceding paragraphs are confined to genetic variation!

Shell Dimensions

ductive isolation is effected by physiological properties which have a genetic basis. Morphological characters are the product of the same gene complex,'' and as long as priority is given to reproductive isolation: ''This inference method is by no means a return to a

Absolute dimensions usually given in taxonomical studies of planorbids are the height and the maximum diameter, height and width of the aperture and the number of whorls. As a measure of flatness the ratio maximum diameter : height is generally indicated. One problem arising in *Gyraulus* and some other genera is caused by the tendency in some groups to deflect the last whorl near the aperture. A slight increase of the deflection angle would result in a highly increased height
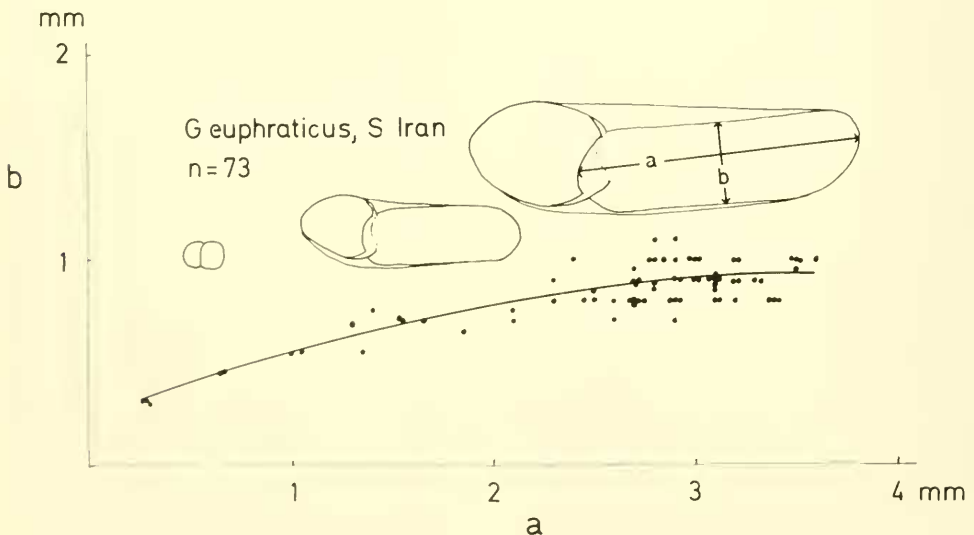

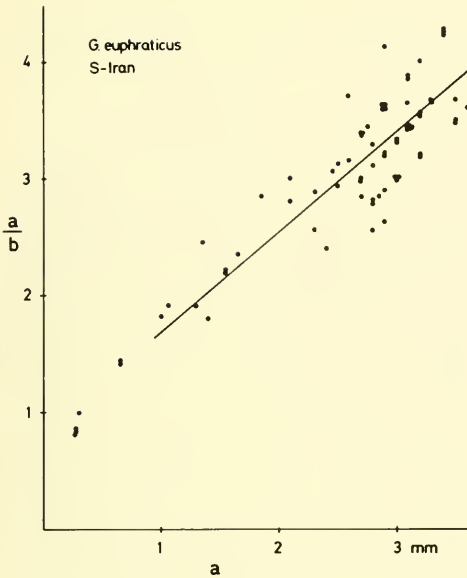FIG. 2. Dimension b plotted against a in a *Gyraulus*.

FIG. 3. Graph with a/b plotted against a and regression line. Same sample as Fig. 2. n = 67 (+6 juv. neglected); y = 0.84 + 0.85x (y = $\frac{a}{b}$, x = a); r = 0.921.

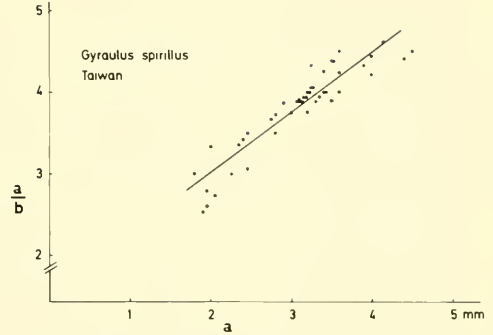
FIG. 4. Same as Fig. 3 but with another species. n = 45; y = 1.55 + 0.73x (y = $\frac{a}{b}$, x = a); r = 0.924.

figure and thus in a falsification of the "flatness index." This is avoided by indicating the maximum diameter minus aperture and the height of the last whorl in its middle as seen in apertural view (Fig. 1A, a and b). These dimensions were first used by Brown & van Eeden (1969: figs. 16, 17), who, moreover, plotted the ratio a/b against a, arguing that the degree of flattening of the whorl during (allometric) growth is thus best demonstrated. These authors have not commented on the question of linearity of such a function.

Growth is allometric since individuals are proportionally high in youth and become proportionally lower during growth (Fig. 2). Plotting absolute dimensions, viz. b against a, yields a distribution of points probably following a hyperbolic function (personal communication by Dr. W. U. an der Heiden, Inst. Biomathematics, Tübingen). Although well-fitting curves in such a graph would give a clear idea of the course of growth, it is impractical to construct them or to find appropriate equations that help in comparing populations. Calculating the ratios a/b and plotting these against a indeed appears to be better suited for these purposes, because at

a > 1 mm, points apparently follow a linear function. Hence regression lines can be drawn and the corresponding equations, y = f + g·x, can be tabulated and compared. *The higher the inclination, indicated by g, the lower the relative increase of dimension b,* or the angle between upper and under sides in the growing shell. *The higher f, indicating the position of the line, the flatter the shell as a whole* (Fig. 109). Linearity of the regression line in a coordinate system with a/b as the y-axis and a as the x-axis was examined by the F-test (Sachs, 1969: 421 *et seq.*). In the two examples (Figs. 3, 4), the critical F-values at the 5%-level (Fig. 3) or at the 10%-level (Fig. 4) were not attained or exceeded; therefore the test did not disprove the linearity of the regression function. Regression lines are compared in cases where critical F-values on the 5%-level are not reached.

There has been some controversial use of the terms upper and under side, due to different orientations—some authors handle planorbid shells as sinistral, most as dextral. It has long been known that all Planorbidae are morphologically sinistral (compare Physidae and Bulininae): genital openings and the anus are on the left. Consequently all *Gyraulus* snails are here considered sinistral.

The number of whorls is determined as usual (Fig. 1B) (Mandahl-Barth, 1954, fig. 2; Pan American Health Organization, 1968: fig. 7). Dimensions, proportions and whorl numbers are important for characterizing species, particularly since they are the main conchological features that, in earlier years, formed the only basis for taxonomy.

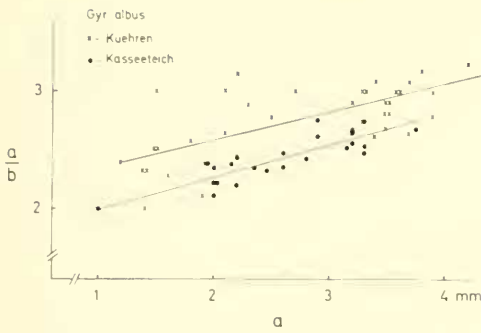As in other groups of fresh-water mol-

FIG. 5.   Variation of a/b plotted against a in two similar biotopes (fish ponds in Holstein, N Germany).

luscs, variation of shell characters within a population is much less than between neighbouring populations, populations being defined as communities of individuals actually interbreeding. Hubendick (1951) convincingly demonstrated this for lymnaeid snails by his "mean photographs."

Intraspecific variation demonstrable with this technique is much less in Planorbidae than in high-spired snail groups, but proportions in two populations of presumably similar biotopes may prove to be so different that their ranges overlap only marginally (Fig. 5). Interpopulational variation of proportions in one species in lakes and in ponds or backwaters is furthermore demonstrated in Fig. 7. Restricted variation is seen particularly in small water bodies where often one or a few individuals have founded a population, which, consequently, has a restricted gene pool (as in cases where the founder-principle becomes effective). Genetic isolation resulting in "a homogeneous genetic constitution" is favoured by self-fertilization of which basommatophoran snails generally are capable (Hubendick, 1951: 31, 32), but probably also by a certain island character of small water bodies (Lassen, 1975; Keddy, 1976; Aho, 1978). The hostile land masses separating ponds and pools may reduce gene flow between limnic populations as compared with gene flow in the vast and continuous populations of many terrestrial animal species. Phenotypic similarity between individuals of such small populations may, furthermore, be caused by the influence of environmental factors that act upon all of them largely to an equal degree, either through selection (e.g. founder effect, as understood by MacArthur & Wilson, 1967:

154, 188) or immediate influence (within the range of reaction norm) upon the growth of individuals.

Non-Genetic Variation of Dimensions and Proportions

Non-genetic variation is due to environmental factors. For any given population it is difficult to assess the influence of selection, as distinct from ecologically induced non-inherited influences, on shell phenotype. For some factors, however, direct action on growth is known. For fresh-water molluscs factors most interacting with shell development are water movement and water chemistry, particularly the calcium content. Calcium deficiency, if not inhibiting occurrence of certain species (Meier-Brook, 1963), may cause shells to become thin and fragile (Hubendick, 1947: 503; Meier-Brook, 1978). Shell thickness in the widely distributed species of *Gyraulus* is, however, regarded not to be significant, neither for taxonomic conclusions nor merely for identification.

Water movement in standing waters generally varies with wind exposure. This means that snails of larger lakes (lotic biotopes) are usually more exposed to water movement than are those in ponds and pools (lenitic biotopes). Reduced shell size in lakes, as shown for *Gyraulus albus* (Figs. 6 and 7), is a plausible consequence, because the planispiral shell offers a large surface to waves. Three ways of size reduction in lotic biotopes are imaginable: (1) Growth generally equals that in lenitic biotopes but individuals die earlier. In this case numbers of whorls must be reduced as well; (2) Snail growth is reduced, because selection has favoured individuals whose diameter grows more slowly; (3) Snail growth is hampered by direct physiological (=non-genetic) action of the environment on each individual. In cases (2) and (3) it could be that whorl numbers are not reduced as compared with snails from still water; then whorls must be narrower and less rapidly increasing.

Fig. 6 depicts ratios of whorl number : diameter in *Gyraulus albus* from some lakes and ponds shows that in these samples situation (1) has not been realized. Whorl numbers are not smaller than in ponds. At least when high whorl numbers (around 4) are reached, pond dwellers have attained more or less greater diameters than lake dwellers. A decision on how far situations (2) or (3) are
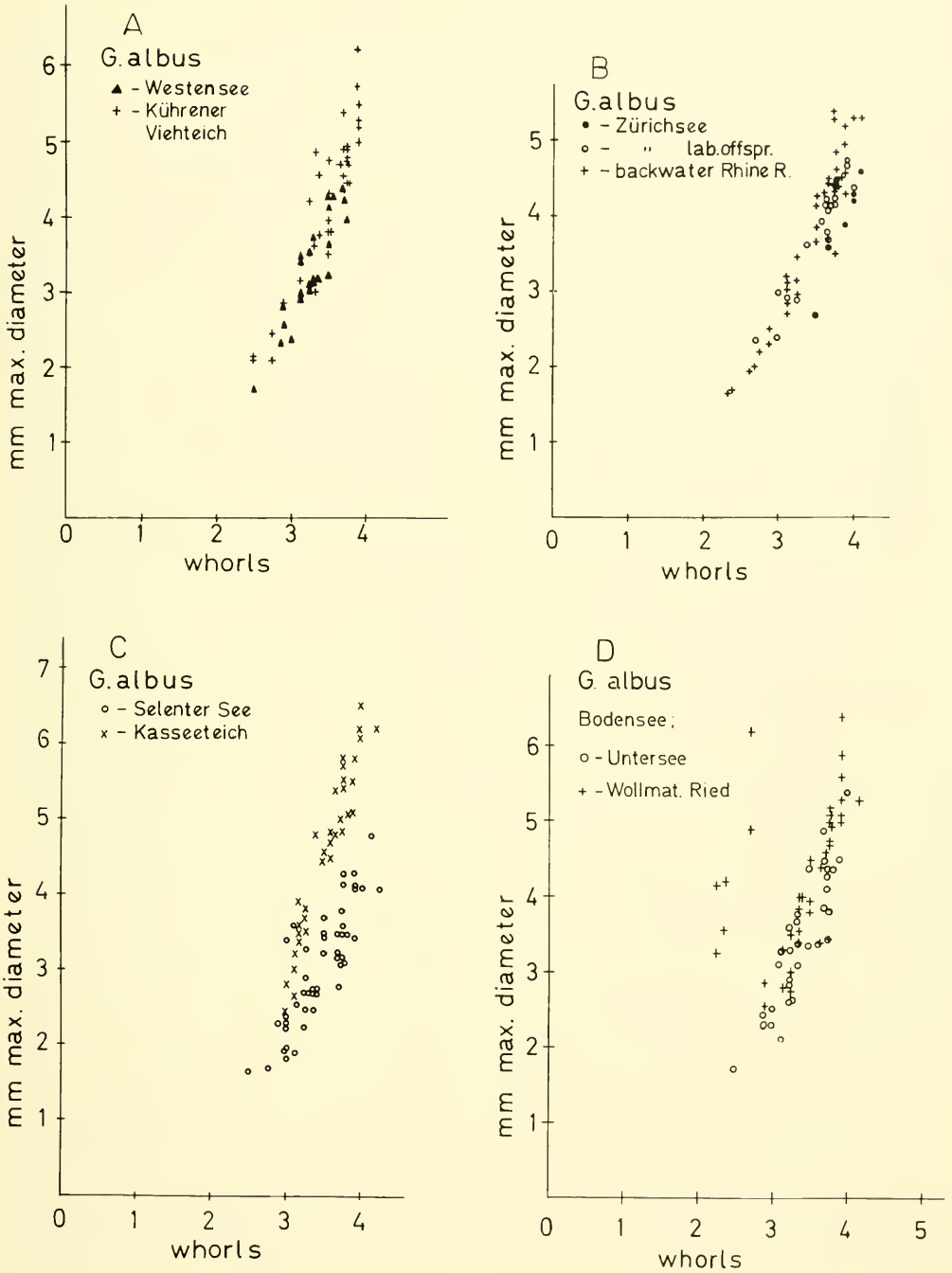
FIG. 6A–D.   Comparison of the ratio maximum diameter : whorl number in lotic (o) and lenitic (x, +) bio-topes. According to the Hotelling-Test (Anderson, 1958) differences between the centroids are highly significant (p < 0.001).
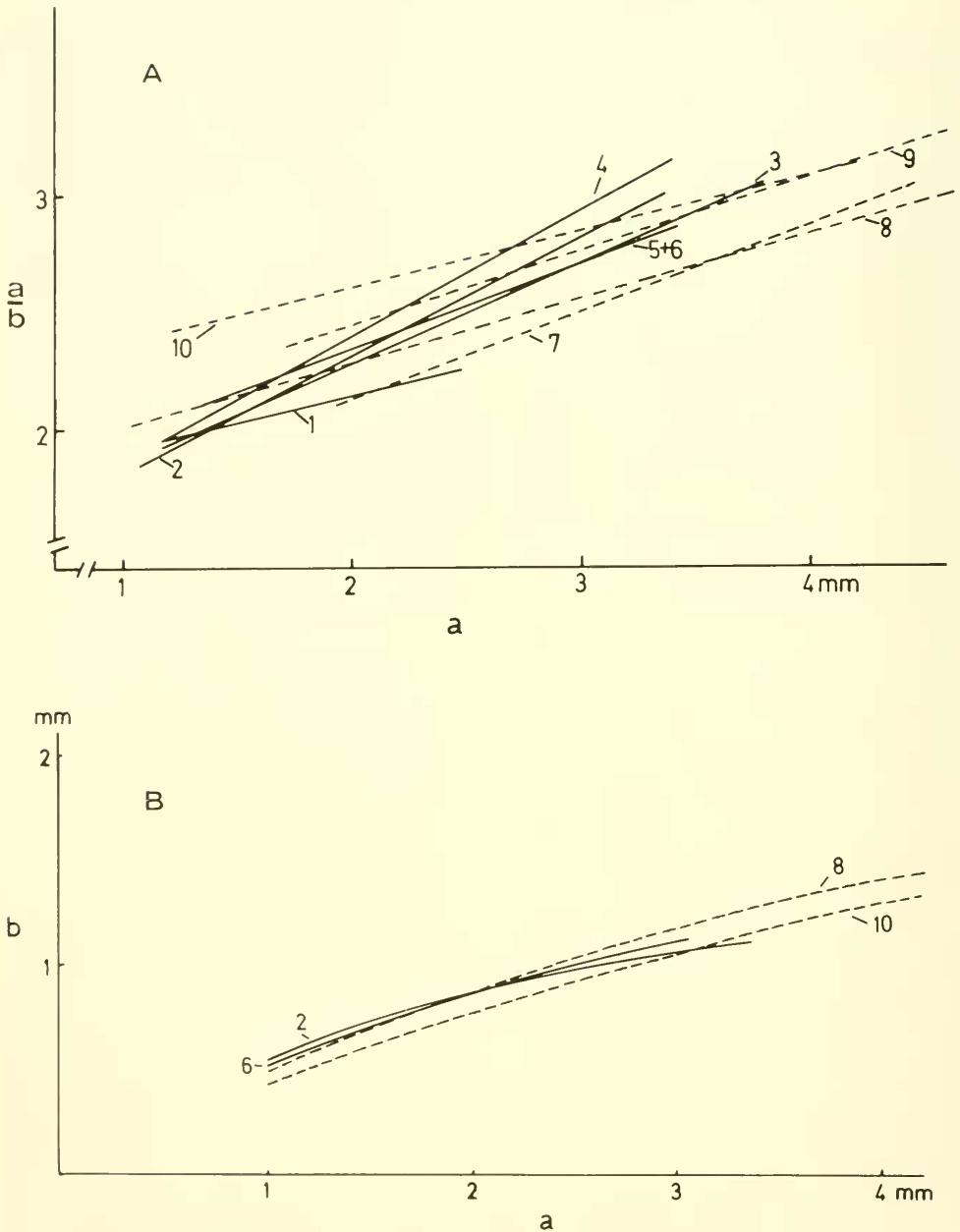
FIG. 7.   *Gyraulus albus*. Comparison of shell proportions between lotic (——) and lenitic (-----) biotopes;
A: a/b plotted against a; B: b plotted against a. 1—Haslacher See; 2—Selenter See; 3—Titisee; 4—
Zürichsee; 5—Lac St. Point; 6—Westensee; 7—Ettenheim; 8—Kasseeteich; 9—Wollmatingen; 10—
Kuehren.

involved in size reduction is not possible
without laboratory breeding experiments. Dif-
ferences between snails collected in Zürich-
see and their offspring reared in aquaria (Fig.

6B) suggest that reduction of shell size is to
some extent reversible and, thus, not inher-
ited. How far genetic fixation of a reduced
shell size in lakes has taken place in other

populations cannot yet be stated. Neither can the rôle of other ecological conditions, e.g. food, be overlooked at present. Large lakes, such as the Bodensee, offer an opportunity for comparing samples from different habitats of the same water body. In Fig. 6D a sample from a wind-exposed shore in Untersee is compared with one from a bay very rich in vegetation (Phragmition and Potamion) and mud. The two biotopes, approximately 5 km from one another are in the same water body. They are lotic and lenitic with broad overlap. However, the difference visible in the other examples is also distinct here, especially in snails with three and four whorls. Probably a steady gene exchange between the two localities takes place, at least in one direction: from Wollmatinger Ried to Niederzell/Untersee a strong current occurs, i.e. toward the outflow of the Rhine River. The strange aberration of six specimens that have attained large diameters despite a low whorl number must thus far remain unexplained. The sample size was not sufficient to support the real existence of a gap between two portions or perhaps generations in the population.

Fig. 6A–C shows, furthermore, that variation of the ratio is greater in lakes than in ponds and other small water bodies. This can have two causes: (1) a larger gene pool in lakes as compared with that in small water bodies (see above: founder principle!), and (2) the fact that every lake has, besides lotic microhabitats, also lenitic ones where vegetation or stones protect animals from direct surf or wave action. Therefore lakes have a greater variety of ecological conditions than ponds, etc., and, consequently, a greater range of ecophenotypes.

One of the other parameters underlying variation is the flatness index (Fig. 7). A comparison of lakes (solid lines) with ponds and similar lenitic biotopes (broken lines) does not bring to light significant differences in the position of regression lines. But there is some evidence that regression coefficients are higher in lakes. What does this mean in terms of shell morphology? In each two examples of lake and pond populations the corresponding curves in a system with a and b as the coordinates (Fig. 7B) show that young snails are slightly higher in lakes than in ponds. The necessity for young and weak snails to increase musculature for increased resistance to moving water may be the cause: bigger muscles in the cephalopedal mass re-

quire a larger volume of the last whorl (the so-called body-whorl) since in danger the latter must be able to take up the whole headfoot complex. For some time b grows well with growing a, but later growth of b is necessarily lowered (otherwise growth would result in snails with two completely conical umbilici). Reduced growth of b gradually takes place when a certain number of whorls is reached. Lake dwellers then usually have a smaller diameter than pond dwellers, as shown above (Fig. 6).

Extreme growth was attained in the laboratory by reducing population density and offering optimal nutrition (food according to Standen, 1949). These giant forms are rarely encountered in nature. Field-collected giant individuals were in some cases trematode-infected. Parasitic castration may be the cause of giantism. Deformations such as open coiling eventually occur. They may be caused by external or internal (genetic) factors and are left out of further consideration here.

Shell Surface

The presence or absence of a peripheral *angle* and a periostracal *fringe* as well as the colour and the presence or absence of spiral striae have been used for species discrimination. Spiral striae, together with growth lines, form a reticulate surface which is appropriately termed ''Gitterskulptur'' in the German literature. A *keel,* typical in *Planorbis carinatus* Müller but also present in the genus *Anisus,* has rarely been developed in *Gyraulus* outside the old lakes (Lakes Prespa, Ohrid, and Biwa).

Some species never produce an angle (example: *Gyraulus albus*, *G. laevis*), others always have an angle (example: *G. riparius*) and usually also a fringe at the same site (*G. tokyoensis*). Species are also found with shells varying from entirely rounded to angulate at the periphery. Thus the absence or presence of an angle may be significant in one group and insignificant in another. The same applies to reticulate sculpture, which is always present e.g. in *G. albus*, always absent e.g. in *G. laevis*, as a rule present in *G. acronicus*, and rarely present in *G. chinensis*.

It must be stressed that embryonic shells (=nuclear whorls of authors) have to be exempted from consideration. On these shells spiral striation occurs in all species examined (Figs. 8 and 47b) including those that are smooth in later stages. Moreover, this micro-
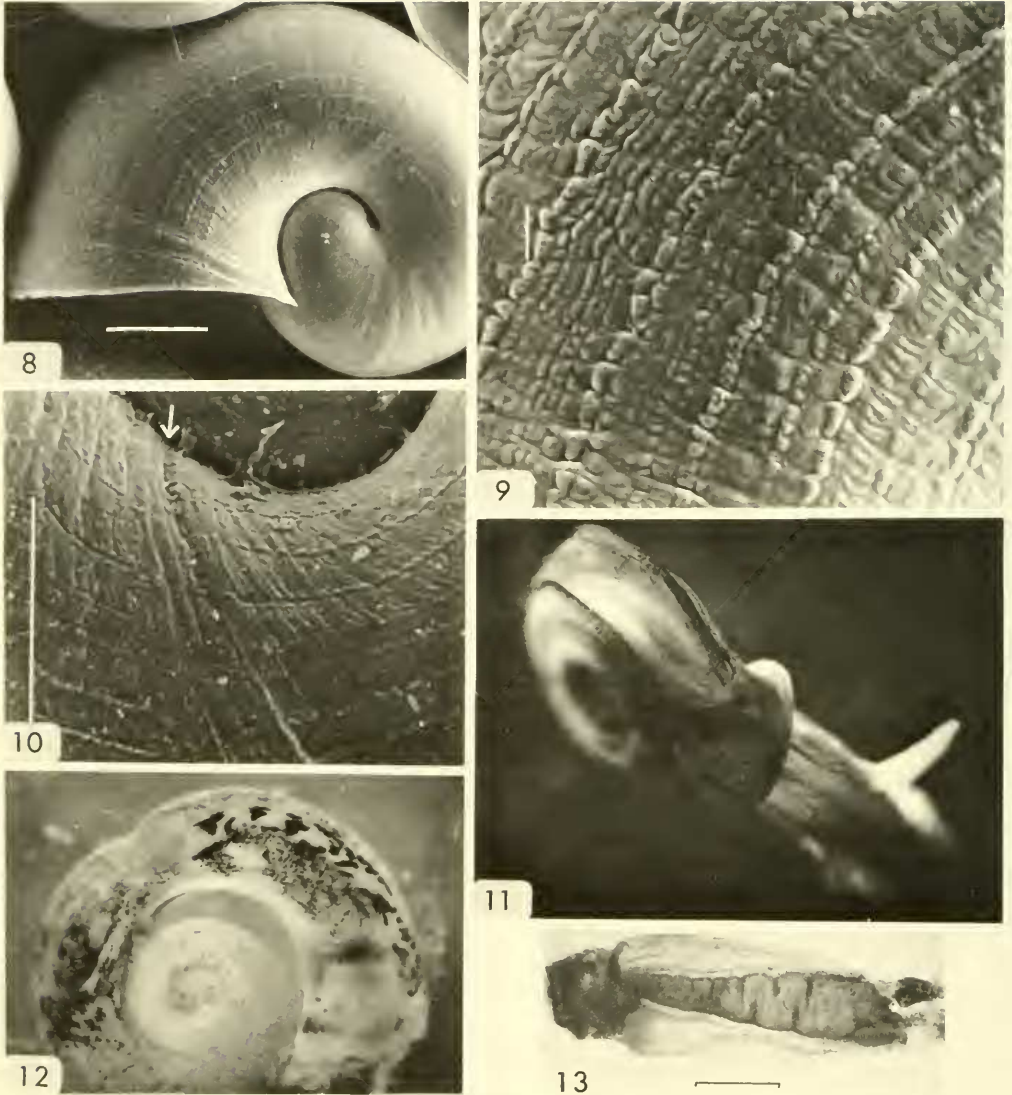
FIGS. 8–13.   8. Shell of freshly hatched individual showing spiral striae. *G. spirillus*, Taiwan. SEM. Scale = 0.1 mm. 9. Part of shell shown in Fig. 8. SEM. Scale = 0.01 mm. 10. Continuation of spiral striae from embryonic to juvenile shell (arrow pointing to transition line between these) in *G. albus*, Zürichsee. SEM. Scale = 0.1 mm. 11. Pigmentation of cephalopedal mass and mantle (diffuse). *G. albus*, Sjaelland. 12. Mantle pigmentation with distinct pattern. *G. chinensis*, Hong Kong. 13. Undulate margins of kidney in *G. parvus*, Speyer.

sculpture was present in all European species examined of *Anisus* s. str., *Planorbis* s. str., as well as in *Armiger* and members of different planorbid tribes (*Hippeutis, Segmentina, Planorbarius*). The distribution of microsculpture in other planorbid groups and in other basommatophoran families has been reviewed by Walter (1962).

Striation on embryonic shells may consist of spirally arranged nodules (Figs. 8, 9) visible in the periostracum, continuous periostracal folds, as shown for *Bulinus tropicus*

(Krauss) by Hamilton-Attwell & van Eeden (1971: fig. 5), round pits ("punctation" in other *Bulinus* spp., Walter, 1962: fig. 1) or regularly spaced transverse (=same direction as growth lines) pits (e.g. in *Biomphalaria glabrata* (Say)).

Though I agree with Walter's (1962: 128) statement "that punctae are lacking in most planorbids," it is likely that the various forms of spiral striation, viz. nodules, folds, round or transverse pits, are not so fundamentally different that a different origin must be assumed. Observations show that folds or initially continuous series of nodules gradually become undulate, loosen to round pits and into transverse pits, which finally become weaker and weaker before totally disappearing during juvenile growth. This can best be observed in *Hippeutis complanatus* (L.) (Meier-Brook, unpublished). Spiral striation of embryonic shells is so universal in various basommatophoran groups that it can be regarded as an ancestral structure. Consequently, smooth or glossy adult shells consistently present in planorbid groups may be regarded as derived from spirally striated ancestors. This view is supported by two facts: (1) striation does not cease abruptly after hatching in adult-smooth groups, but is continued onto the first parts of the juvenile shell; (2) in these as well as in adult-striated groups postembryonic striae form an immediate continuation of embryonic striae (e.g. in *Gyraulus albus,* Fig. 10).

Gyraulus costulatus from Liberia was reported as having "a total lack of punctation" (Walter, 1962: 128). Examination of the same species, also from Liberia, revealed that continuous striae are present on the nuclear whorl, which later (but still before hatching) break up into small nodules similar to those in *G. spirillus* and other species.

Reticulate sculpture on the shell surface is sometimes, though not necessarily, accompanied by hair-like protrusions formed by the periostracum. They regularly occur in *Gyraulus albus* (Fig. 36) and occasionally in *G. acronicus* (Fig. 62B).

Wherever peculiar periostracal structures occur in *Gyraulus,* corresponding, but weaker, shell sculpture is found below these. A peripheral fringe of periostracum never decorates an equally rounded periphery; striated periostracum does not cover a completely smooth shell surface, as could be shown in shells devoid of their periostracum. Below a distinct fringe there is at least a distinct peripheral angle, if not even a keel (Fig. 87).

Thickness of shells was not measured. Unusual thickness probably plays a rôle only in ancient lakes where additional angles and keels can be used to characterize species.

Shell color varies from light corneous to reddish brown to light brown, but the color range is too narrow to provide reliable characters for species determination. The degree of transparency is apparently also of equally low value.

There were no apparent correlations between shell surface characters and environmental conditions except where the reticulate sculpture was slightly worn in surf zones of sandy lake shores.

Body Pigmentation

Pigmentation of the cephalopedal mass shows slight variation, from colorless with scattered spots (Fig. 89) to homogeneously light grey. However, pigmentation of the mantle roof in most cases can be categorized (1) as diffuse and with poor contrast (example *Gyraulus albus,* Fig. 11) or (2) with distinct patterns, and thus with rich contrast (example *G. chinensis,* Fig. 12). These patterns are most distinct on the right side between the kidney and the darker region where the prostate gland, uterus and oesophagus run along the inner side of the whorl. Although pigment patterns are highly variable, there were usually no doubts about which category was involved. In *G. acronicus* the pigment pattern is not as rich in contrast as in *G. chinensis*; in some populations of *G. acronicus* a clear decision was impossible and identification had to be based on other characters (shell, male copulatory organ). But as a rule the nature of mantle pigmentation can readily be categorized and serves as a helpful character.

Pallial Organs

The only pallial organ that proved to have a shape characteristic for certain taxa is the kidney. It has conspicuously "undulate" margins (Fig. 13) in some species, whereas in most species the margins are straight. In unrelaxed individuals the margins of the shrunken kidney seemed to be more or less undulate in all species (perhaps the reason that the significance of this peculiarity has gone unreported, e.g. Hubendick (1955: 456)
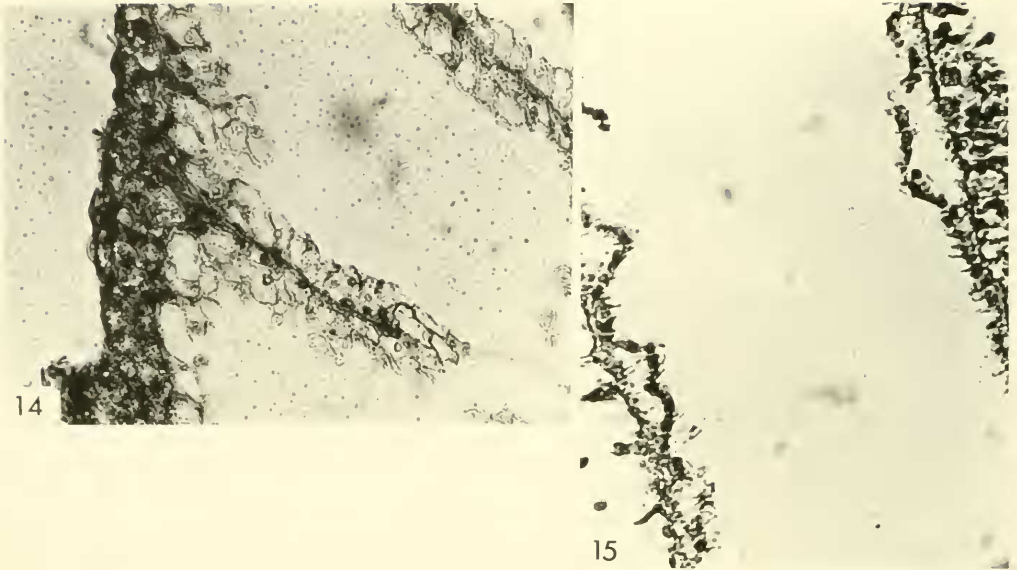
FIGS. 14–15. 14. Septate kidney in tangential section. *G. laevis*, Kuehren. Hematoxylin and eosin. (M 123). 15. Non-septate kidney in tangential section. *G. euphraticus,* S Iran. Hematoxylin and eosin. (M 140).

stressed "that details of the form and size of the kidney are . . . not reliable as taxonomic characters"). In individuals fixed after relaxation as well as in living ones, however, the difference is obvious. Histological investigation revealed that in *Gyraulus laevis* and *G. parvus* (Say) real septa protrude into the renal lumen alternating from both sides. Probably these septa have developed from folds of the renal walls, but fusion (Fig. 14) has taken place that is evidently irreversible. No such septa can be detected in most other species (Fig. 15), even when contraction yields a form like "undulate" margins.

Alimentary Tract

The jaw and radula have long been the main non-conchological characters used in gastropod taxonomy. In rare cases, however, these parts have contributed to differential diagnosis at the infrageneric level. This is the situation in *Gyraulus.* Except for a small group of species endemic to ancient lakes in Macedonia, radular teeth are uniform throughout the genus. Should species differences really occur these must be so insignificant that they are masked by individual variation. Although great hopes used to be placed on the radula for species discrimination, many

authors (e.g. Annandale & Rao, 1925; Roszkowski, 1929; Wagner, 1931) came to the same conclusion: the value of the radula for species discrimination has been exaggerated. Most regrettably variation of radular characters is not quantifiable in our genus, so that the above statements could only be supported by a great number of additional figures. SEM micrographs of radulae documenting its low value have been deposited at the Senckenberg-Museum, Frankfurt.

On this occasion it is necessary to caution against misinterpretations of scanning electron micrographs. Owing to the great depth of focus it is very difficult to tell the degree of inclination of part of a radula. To demonstrate the effect of varying directions of observation two micrographs of the same region of one individual radula is shown (Fig. 16). Hence, statements about "long" and "short" cusps on radulae, judged from SEM photos, should be regarded with caution. Furthermore differences occur between younger and older portions of a radula where teeth are worn and, thus, may lack the sharp edges of their cusps (Fig. 17). To save space I refrain from giving descriptions of radular teeth for all species except for the type-species of the genus and the aberrant species from ancient lakes. The number of teeth per
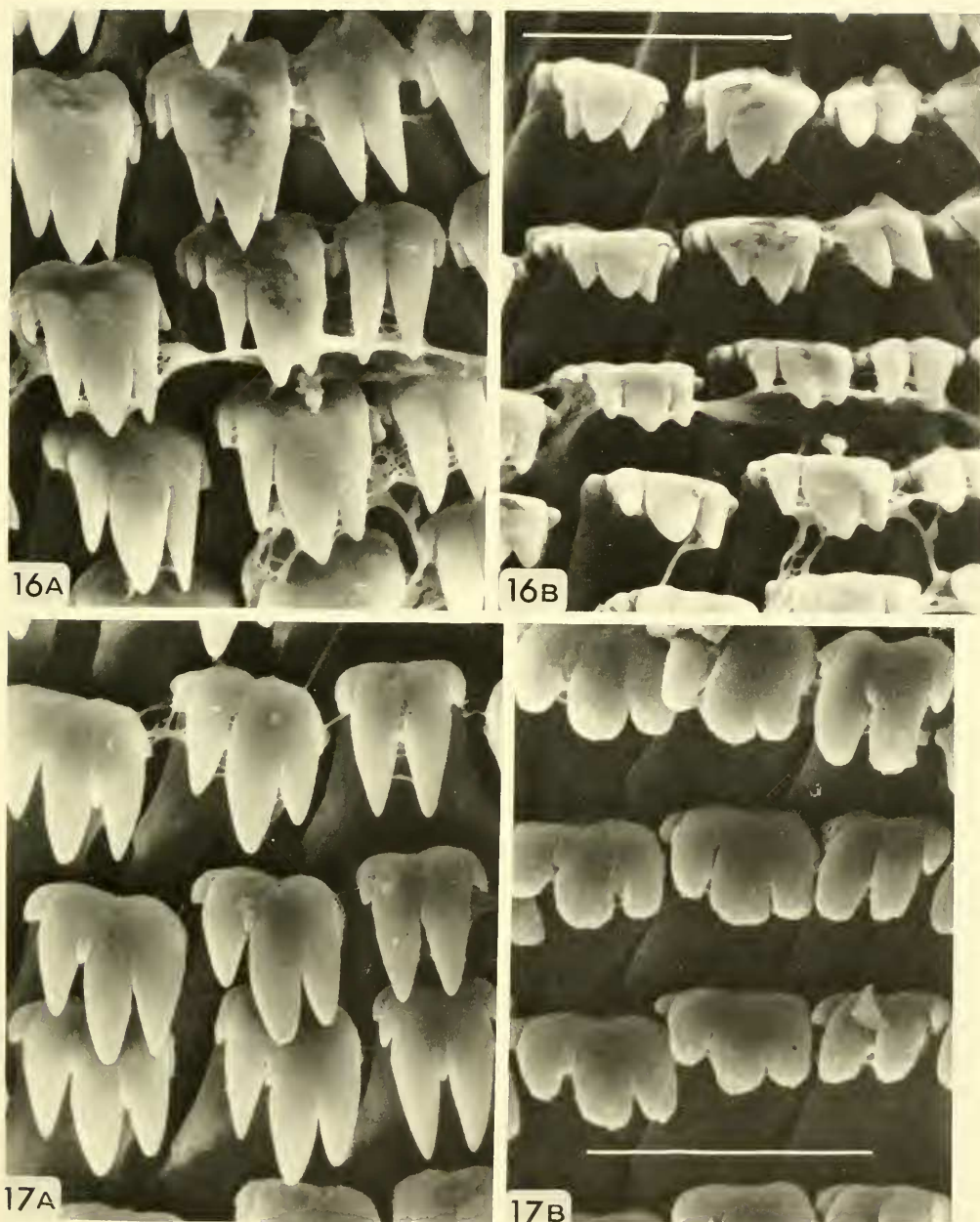
FIGS. 16–17. 16. Identical part of radula in perpendicular view (A) and with 37° inclination (B). *G. parvus,* W Iceland. SEM. Scale = 0.01 mm. 17. Unworn (A) and worn (B) central and lateral teeth in different regions of the same radula. *G. albus,* Sjaelland. SEM. Scale = 0.01 mm.

transverse row appears to be highly size-dependent and is almost worthless for taxonomic purposes (Bertram & Meier-Brook, in preparation).

The oesophagus, crop, stomach, caecum, and digestive gland are devoid of taxonomically significant characters within our genus. Striking variation occurs in the size and form
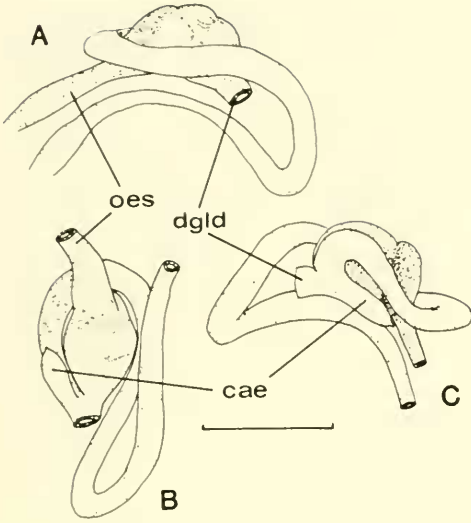
FIG. 18.   Intestinal loop, viewed from the left (A), ventral view (B) and viewed from the right (C). *G. albus*, Sjaelland (M 286).

of the intestinal loop. Normally (Fig. 18) the intestine, after leaving the pyloric region of the stomach, runs anteriad on the right side of the animal, bends to the left, passes over the oesophagus, bends once more, runs backward on the left side, forms an elongate loop embedded in the large digestive gland, and finally runs anteriorly after passing the stomach on its left side again, to terminate as the rectum. In portions of the lots examined of *Gyraulus laevis* and in all specimens dissected of *G. parvus* the loop was absent, and the intestine showed only a slight indication of flexure where the loop is usually intercalated (Fig. 19A, arrow). Transitional stages occur. Presence or absence of a loop is not strongly correlated with more invariable species characters and, thus, is not considered to be a reliable character. In most species presence and absence seems to be randomly distributed, even within the same population. In a few species percent omission is increased (e.g. *G. parvus*); in others the loop is well developed in all individuals examined (e.g. *G. acronicus, G. rossmaessleri*). Therefore, in certain cases presence or absence of an intestinal loop may serve as a supporting character, and in future studies further attention should be devoted to it. Richards (1973a), studying *Biomphalaria glabrata* with both absence and presence of a
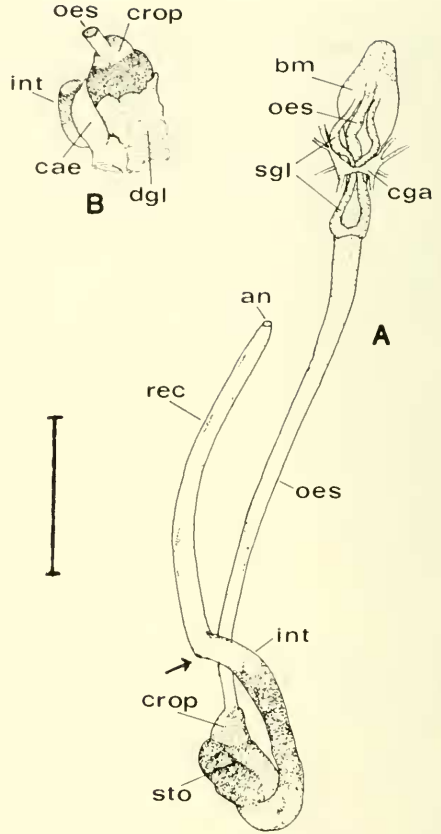

FIG. 19.   (A) Omission of intestinal loop, *G. laevis*, Kuehren. The arrow indicates the site at which a loop usually is intercalated. (B) Same; stomach region in ventral view. Key to lettering p. 27.

loop in the same stock, found that omission is inherited. This may be the case in *Gyraulus* also, but inheritance, of course, does not necessarily mean taxonomic significance.

Reproductive Organs

The number of lobes in the ovotestis (hermaphroditic gland), a character used in the taxonomy of at least one group of planorbid snails, viz. *Biomphalaria* (e.g. by Paraense, 1966; Pan American Health Organization, 1968), is difficult to determine, because the lobes are insufficiently differentiated in the most apical portion of the ovotestis. The value of lobe numbers is especially low if variation between species is low and there is overlap; this is the case in *Gyraulus* (mostly between 28 and 32).

The length of the spermoviduct (hermaph-roditic duct) (sod in Fig. 43) and of its parts has not proven to be of value as a character, particularly since the seminal vesicle can be lengthened by stretching to more than twice its dimension in the resting state. The shape of the seminal vesicle coils may be charac-teristic, being either rounded and bulbous or more delicate and studded with spiny humps (Fig. 20). Though in many cases a decision is difficult, extreme formations can be found to be constant.

The seminal vesicle (vs in Figs. 43, 57) can be exceptionally voluminous and appear larg-er than the prostate gland and uterus togeth-er (e.g. *Gyraulus riparius*). The portion of the spermoviduct between the seminal vesicle and the carrefour (=distal spermoviduct), which is usually very thin, in certain cases can be wider than the vas deferens and may then have diagnostic value (e.g. *G. laevis*).

In the carrefour (car in Fig. 43) and the parts of the female tract down to the vagina (vag in Fig. 43), no characters useful for taxonom-ic purposes have been found. The vagina in many cases is much inflated, partly below the zone of fusion with the duct of the bursa cop-ulatrix. This inflation may be absent, but it has, as yet, been impossible to recognize any regularity. Intra- and interpopulational varia-tion of the bursa copulatrix and its duct are usually greater than interspecific variation. Therefore it has lower value than in other planorbid genera (e.g. *Planorbis*, Meier-Brook, 1976c), but an extremely slender bursa (e.g. *Gyraulus laevis, G. parvus*) or an unusually inflated one (e.g. *G. eugyne* n. sp.) is a good species character.

In the male reproductive tract the length of the free sperm duct (free spd in Fig. 48), rel-ative to other parameters, is of restricted val-ue, but the prostate gland has been judged as bearing one of the most reliable charac-ters for species discrimination in the genus since counting the numbers of diverticula was introduced into taxonomic work (Baker, 1945; Meier-Brook, 1964; Brown & van Eeden, 1969; Pace, 1973). Numbers of diverticula extend over a wide range in the genus, from <10 to >30, and they can be determined without trouble (Tables 1 and 2). They are rendered invaluable, because they appear to be age—or size—independent (Fig. 21). In immature individuals diverticula may be diffi-cult to recognize, but they are formed in de-finitive number early in ontogeny. Variation generally is low enough to permit the indica-
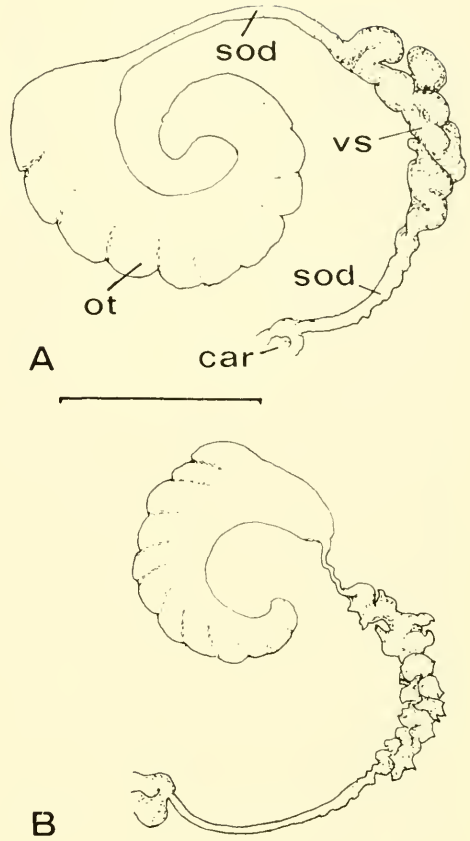

FIG. 20.   Coiling of seminal vesicle: bulbous (A; *G. parvus,* Speyer) (M 275); spinous (B; *G. hieman-tium,* Hanechi-son) (M 260).

tion of mean diverticula numbers even in smaller samples (Fig. 22). Diverticula are usu-ally unbranched, except the most distal one, two or three, which may incidentally be bi-fid. The remaining diverticula were almost ex-clusively found unbranched in most species (e.g. *Gyraulus acronicus, G. euphraticus* (Mousson)). Here and there, along the whole prostate, bifid diverticula were regularly no-ticed in *G. parvus* (Fig. 50). Another constant feature in the prostate gland is the mode of grouping. Diverticula are usually spaced closely and regularly (Fig. 23), whereas in certain groups they emerge from the pros-tate duct with gaps and in changing direc-tions (e.g. *G. laevis, G. parvus,* Figs. 48, 50).

The length of the vas deferens is occasion-ally useful as a standard parameter for com-parison with the proper male copulatory or-

TABLE 1. Reproductive organs of *Gyraulus albus*. Data from Meier-Brook (1964) are included.

Locality	No. prost. divert.			Male copulatory organ					Bursa copulatrix	
				Total length (mm)			Ratio psh:prp			
	n	range	x̄ ± s.d.	n	range	x + s.d.	range	x̄ ± s.d.	clb. el.	clb. sph.
Sjaelland	18	7–16	11.9 ± 3.6	14	0.8–1.3	1.0 ± 0.1	1.2–1.8	1.6 ± 0.2	+	
Bodensee	—	(indiscernible)		2	0.9 + 1.4		1.3 + 1.4		+	
Zürichsee	3	17 + 19 + 20		3	1.4 + 1.4 + 1.0					+
Greifensee	3	16 + 18 + 18		3	1.4 + 1.2 + 1.7		2.0 + 2.0 + 2.0			+
Fischau	1	8		4	0.9–1.2	1.0	1.4–1.7	1.5	+	
Ursee	—	(indiscernible)		6	1.1–1.5	1.3 ± 0.1	1.4–2.2	1.9 ± 0.3	+	
Kuehren	2	13 + 15		1	0.9		2.0		+	+
Wollmatingen	—	(indiscernible)		2	1.8 + 1.5		1.3 + 1.2		+	
Ettenheim	4	15–22	17.5	4	1.3–1.8	1.6	1.4–2.0	1.7	+	
Windgfällw.	—	(indiscernible)		4	1.3–1.5	1.4	1.6–1.8	1.8		
Total	31	7–22	13.8 ± 4.3	43	0.8–1.8	1.2 ± 0.3	1.2–2.2	1.6 ± 0.3		
excl. Sjaell.	13	8–22	16.5 ± 3.5	29	0.9–1.8	1.3 ± 0.3	1.2–2.2	1.7 ± 0.3		

TABLE 2. Characters of *Gyraulus* in Europe and N Asia; spt. ki. = septate kidney.

Species	No. prost. divert.			Male copulatory organ					spt. ki.
				Total length (mm)			Ratio psh:prp		
	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.	
albus (Table 2)	31	7–22	13.8 ± 4.3	43	0.8–1.8	1.2 ± 0.3	1.2–2.2	1.6 ± 0.3	
laevis, Kuehr.	9	9–15	12.4 ± 2.7	11	1.0–1.7	1.3 ± 0.2	1.2–2.5	1.9 ± 0.4	+
laevis, Haarl.	7	6–13	9.1 ± 2.7	11	0.6–1.9	0.9 ± 0.4	1.0–2.1	1.6 ± 0.3	+
parvus, centr. Eur.	15	9–17	12.1 ± 2.5	15	0.9–2.0	1.4 ± 0.3	1.2–2.3	1.6 ± 0.3	+
parvus, Iceld.	9	6–14	10.7 ± 2.7	11	1.0–1.6	1.35 ± 0.2	1.5–2.5	2.0 ± 0.3	+
rossm., Alsace	12	8–14	11.3 ± 2.1	14	1.1–2.0	1.4 ± 0.3	0.4–0.6	0.5 ± 0.1	+
rossm., Pl. W.[1]	7	15–21	18.2 ± 2.2	7	1.8–2.3	2.0 ± 0.2	0.3–0.4	0.35 ± 0.0	+
riparius	4	7–10	8.3	4	0.7–0.9	0.8	0.6–0.9	0.75	+
crista, Kuehr.		see text p. 42		11	0.6–1.0	0.8 ± 0.2	1.1–2.4	1.5 ± 0.4	+
acron., centr. Eur.	15	21–39	26.9 ± 5.3	16	2.1–4.7	3.5 ± 1.0	1.2–1.7	1.5 ± 0.2	+
acron., N Eur. + As.[1]	13	20–30	25.3 ± 3.1	25	1.9–3.2	2.5 ± 0.4	1.1–2.4	1.5 ± 0.3	−

[1] Unrelaxed.
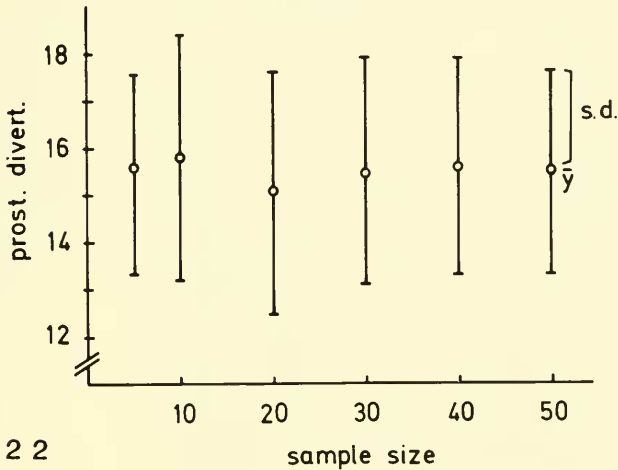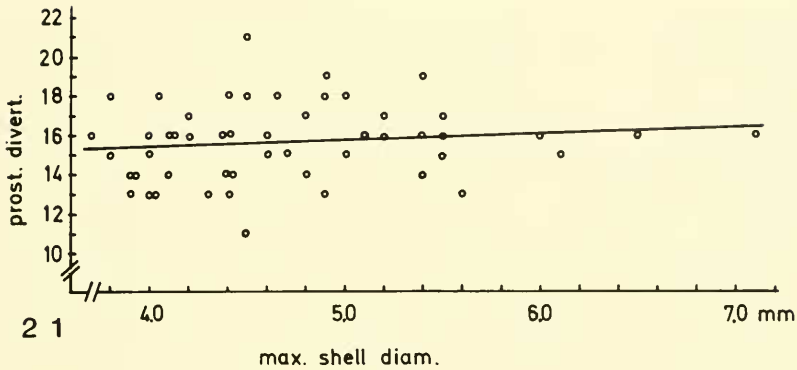
FIGS. 21–22. 21. Numbers of prostate diverticula in snails of various sizes. *G. spirillus*, Taiwan. y = 14.1 + 0.33x; n = 51; r = 0.1245 (significance limit for p = 0.1 is 0.2329). 22. Progress of mean numbers of prostate diverticula and standard deviations with increasing sample size. *G. spirillus*, Taiwan.

gan because it is a nonmuscular organ and, thus, not subject to contraction during fixation (Meier-Brook, 1976b). In *Gyraulus* the length could not be determined exactly in the majority of cases. Delamination is easy in *Planorbis* (Meier-Brook, 1976c; fig. 1), namely between the upper end of the penis sheath and the point of fusion of the sperm duct and the prostate duct. In *Gyraulus* this point is much less discernible.

The width of the vas deferens is uniformly low through the vast majority of *Gyraulus* species, but in some species from Lake Ohrid and the Malayan Archipelago it is constantly greater, and in one species (*G. parvus*) in the proximal half it is ⅓ to ½ of that in the distal half (both measured in the middle, Fig. 51). In these few cases characters of the vas deferens can serve for the discrimination of taxa.

The form and total length of the male copulatory organ as well as the ratio of length of penis sheath : length of preputium are of great taxonomic value and have been highly valued in planorbid taxonomy since they were used for discriminating among *G. acronicus*, *G. rossmaessleri* and *G. albus* (Meier-Brook, 1964; Hudec, 1967; Brown & van Eeden, 1969). This is in contradiction to Hubendick's (1955: 457 *et seq.*) opinion that it is "worthless to make measurements of its (male copulatory organ) different parts and then to base comparisons on details of proportion." The total length can be related to other dimensions and expressed by indicating the position of its upper end in relaxed individuals in situ (Fig. 44; Meier-Brook, 1964: figs. 21, 22). The ratio total length of the ♂ copulatory organ : greatest width of penis sheath, as
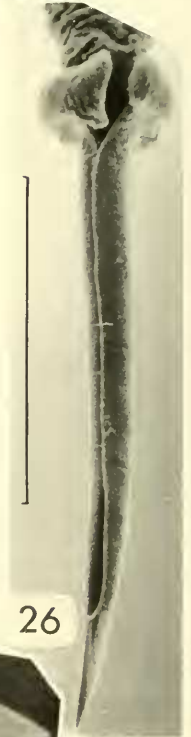
tentatively used in a previous paper (Meier-Brook, 1964), is considered to be unnecessary, since drawings demonstrate differences better than numerical data in this case.

The penis provides two significant characters: the position of the penis pore, i.e. the aperture of the sperm canal and the shape of the penis tip. The penis tip is usually equipped with a bulbous thickening, resembling the mammalian glans penis (Fig. 45, etc.); in a few groups the thickening may be less distinct, in others there is a conical narrowing instead of a thickening (e.g. in *Gyraulus rossmaessleri,* Fig. 55; Meier-Brook, 1964: figs. 24, 27). The penis pore almost always is situated near or in the bulbous thickening and generally has a well defined site: (1) subterminal or in the distal half of the thickening (*G. albus*), (2) near the proximal end of the thickening or in its upper half (*G. acronicus,* almost all groups from S and SE Asia). Rarely it is situated above the middle of the whole penis, as described for *G. lychnidicus* by Hubendick & Radoman (1959: 236) and observed in the present study only in *G. malayensis* n. sp. from Bali, Java and Malaysia. In every case there is a more or less wide open groove running down from the penis pore to the proximal opening of the stylet (Fig. 24). During copulation the sperm traverses the groove to the stylet. The stylet leads it out of the everted copulatory organ through the hole in the papilla (Fig. 29). The stylet is so uniform in the whole genus as well as in closely related genera that it is not attributed interspecific significance, except in a few cases where it is reduced in size and form: the "hob-nail stylet" of *G. rossmaessleri, G. riparius,* and *G. crista* (L.).

Hubendick & Radoman (1959: 231–234) report on differences between two species, *G. crenophilus* Hubendick & Radoman and *G. fontinalis* Hubendick & Radoman, in the proximal end of the stylet. The basal part is said to have chitinized internal bars in the one

and no such bars in the other species. When these species are reexamined, attention should be directed towards these alleged differences. According to my experiences such differences could occur depending on where one happens to section. In the middle of the wider basis (Fig. 25) a cross section may look like a horseshoe, as stated for *G. fontinalis* (Hubendick & Radoman, 1959: 234); a few μm towards the penis tissue the picture should be quite different. A continuous series of sections might have been impossible at that time because of the resistant stylet material.

The basal opening may vary a little from comparatively wide to narrower (Fig. 26). This figure, by the way, clearly demonstrates that the stylet is a hollow tube formed out of a thin blade by rolling up in a clockwise sense. The sperm leaves the stylet through a slit left open near the stylet tip (Fig. 27), which in this view appears extremely acute although it is of lancet-shape when viewed after being turned 90° (Fig. 28). In everted organs of individuals of various species only this tiny stylet tip penetrated the hole in the papilla (Brown & van Eeden, 1969, fig. 6). This hole (Fig. 29) is so small that most of the stylet (including its base) probably cannot pass through it, not to mention the penis tip itself. However, a penis extending into the preputium has been reported by Wright (1963: 463) as a characteristic of *Gyraulus costulatus* from Angola. Unfortunately he did not mention how frequently this condition was seen. I have found no more than one such case, which I could not explain, in adult *Gyraulus.*

In immature animals the stylet is positioned in the distal portion of the ♂ copulatory organ; this is the rule. In early stages of development there is no clear distinction between the future penis sheath and the preputium. The developing penis with the stylet, which is formed in its definitive size (Hubendick, 1958: 429; Meier-Brook, 1964: 238), extends distally to near the male genital pore.

←

FIGS. 23–28.   23. Prostate gland with closely spaced diverticula. *G. spirillus,* Taiwan. Most distal diverticulum two-branched, others unbranched. CPD; SEM. Scale = 0.1 mm. 24. Penis pore (arrow) and groove leading to stylet aperture. *G. euphraticus,* S Iran. CPD; SEM. Scale = 0.01 mm. 25. Stylet base is "horseshoe-shaped" in cross section. *G. chinensis,* Chongpyong. SEM. Scale = 0.01 mm. 26. Stylet showing apertures and edge of rolled up blade. *G. euphraticus,* S Iran. CPD; SEM. Scale = 0.1 mm. 27. Distal aperture of stylet. *G. euphraticus,* S Iran, different individual. CPD; SEM. Scale = 0.01 mm. 28. Penis tip showing penis pore (arrow) and stylet with basal aperture and lancet tip. *G. euphraticus,* S Iran, same spec. as in Fig. 26. CPD; SEM. Scale = 0.1 mm.

FIG. 29. Papilla showing hole through which the stylet tip is pushed for copulation. Copulatory organ broken between papilla and diaphragm. *G. spirillus,* Taiwan. CPD; SEM. Scale = 0.01 mm.

Later, when the copulatory organ begins to differentiate the stylet is still seen in the preputium surrounded by the tissue producing it (Meier-Brook, 1964, fig. 35).

During longitudinal growth of the whole organ the penis tip and the stylet then gradually withdraw, before differentiation of papilla and diaphragm takes place. In trematode-infected individuals, which were externally adult, but occasionally retarded in sexual development (microphally), I have observed portions of the penis extended into the preputium. Possibly an event like parasite-induced retardation would also explain Wright's (1963) statement. This is regarded the more probable since Brown & van Eeden (1969), investigating a large series of specimens of *G. costulatus* (Krauss) from South Africa, did not find the stylet position noticed by Wright.

In immature snails the stylet may be unrecognizable until a rather late developmental stage. This was first observed in *G. parvus* from Speyer (Germany). The first specimens received appeared to be fully grown. Notwithstanding, a stylet could not be detected, and the snails were tentatively placed in the genus *Promenetus.* In a few specimens the distal area of the penis sheath was found chitinized internally, a condition never reported in the literature. After keeping the remaining snails in aquaria for some weeks, all devel-

oped a normal stylet, while the chitinized region of the penis sheath was no longer observed. The shells had not noticeably grown in the meantime but body pigmentation had turned dark. The phenomenon, subsequently also found in *G. parvus* from Iceland and *G. laevis* from Germany, has not been investigated further. Observations suggest that the development of the stylet in these two species does not follow the pattern described for other species by Hubendick (1958) and confirmed in the majority of *Gyraulus* species in the present and a previous study (Meier-Brook, 1964). Possible differences in the site and mode of stylet formation that should be studied in detail may prove to support other differences on the subgeneric level. They are not so different that stylets in the differing groups could be regarded to be non-homologous. Otherwise, *G. parvus* and *G. laevis* could not be placed in the genus *Gyraulus.*

Any consistent lack of a distinct stylet in a species would indicate that it does not belong in the genus *Gyraulus.* Several African planorbid species were previously placed in *Gyraulus* and its close relative, *Anisus,* on conchological grounds, but in spite of the lack of a stylet. They have later turned out to be members of two separate genera, described as new by Brown & Mandahl-Barth (1973).

In two of three new *Gyraulus* species described by Brandt (1974: 241–243) the penis is said to lack a stylet. Anatomical features of these species are not figured; therefore it is impossible to determine their generic position.

Other species previously regarded as *Gyraulus,* but devoid of a penial stylet, could be placed in *Planorbis,* e.g. *Gyraulus macedonicus* Sturany (Hubendick & Radoman, 1959: 243), *G. presbensis* Sturany and *G. intermixtus* Mousson (Meier-Brook, 1976c).

The preputium usually contains two muscular pilasters, formed as an invagination of the preputial inner epithelium (cf. Meier-Brook, 1964: figs. 28–31). The interspace is filled with parenchyma, sufficiently extensible to permit eversion of the preputium for copulation. Presence and site of pilasters are normally indicated in external view by a particularly dense longitudinal pigmentation of the preputium. This pigmentation is evidently a result of folding of an outer epithelium which is rich in pigment anyway. In species with small ♂ copulatory organs pilasters may be absent. Doubtful cases occur and are exclud-
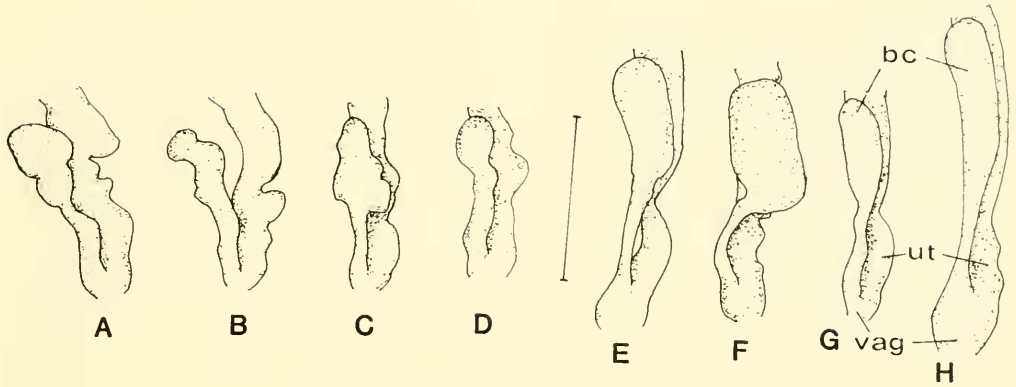
FIG. 30.   Shapes of vagina and bursa copulatrix in contracted (A–D) and extended (E–H) individuals of *G. spirillus*, Taiwan.

ed from decisions. Clear absence may be consistent and is then used for characterizing species (compare also definitions!).

Non-Genetic Variation in
Reproductive Organs

Effects of Fixation.—Since form and dimensions of soft parts underlie different amounts of contraction depending on fixing conditions it was necessary to evaluate the rôle of preparation methods commonly used.

Anatomical characters generally used in taxonomical studies of planorbid snails were compared in (1) individuals killed by immersion in 70% ethanol and in (2) those killed in warm (60–70°C) 4% formalin after relaxation with pentobarbital (according to Meier-Brook, 1976a, 1976b) for 12 hr. Both cohorts were selected at random from the same stock of laboratory reared snails. Comparison was made as to the shape of the bursa copulatrix and vagina and to the proportions of parts of the ♂ copulatory organ.

The bursa copulatrix in the example used (*Gyraulus spirillus* from Taiwan) has a more irregular shape in contracted (unrelaxed) individuals than in extended (relaxed) ones (Fig. 30) and is smaller. These alterations are evidently caused by external pressure exerted by surrounding tissues of the shrinking animals. Active contraction is unlikely because this organ lacks muscular tissue.

While the preputium (prp in Table 3) loses an insignificant portion of its length, it is mainly the penis sheath (psh in Table 3) that is reduced in length by 25% on average. Con-

sequently the ratio psh:prp is also altered significantly. These results differ from those found in a *Planorbis* species (Meier-Brook, 1976b), where the penis sheath is smaller and much less muscularized. Why the preputium in *Gyraulus* contracted to a lesser degree than expected after the experiences with *Planorbis* is not clear. Histologically these parts do not differ fundamentally in the two genera. There is good reason not to transfer exact data of length reduction from *Gyraulus spirillus* to other species of the genus.

Alterations not given in the table are seen in the length and shape of the penis (Fig. 31). The penis in most cases coils within the penis sheath, which, in its turn, shortens and widens by contraction of the spirally arranged longitudinal musculature (Fig. 32).

Circulatory and Nervous Systems

The circulatory and nervous systems of all groups have been examined for taxonomically valuable characters. I examined the heart, sections of the aorta, and the central nervous system. There were no unique character states enabling species discrimination. Dense pigmentation of the heart is constant in *Gyraulus laevis*, rendering the heart the darkest part of the animal beside the stomach and parts of the intestine. The heart has little pigmentation or is unpigmented in all other species studied.

Chromosomes

The karyotype has proved useful in some planorbid groups, particularly in the problem-

TABLE 3. Dimensions (mm) and ratios of parts of the male copulatory organ in *G. spirillus* from Taiwan, fixed in relaxed (fully extended) and unrelaxed (contracted) states.

Fixing state	n	Whorl number x̄ ± s.d.	Length of psh x̄ ± s.d.	t-test p	Length of prp x̄ ± s.d.	t-test p	Ratio psh:prp x̄ ± s.d.	t-test p
fully extended	21	4.11 ± 0.32	1.21 ± 0.20 (range 0.8–1.5)	< 0.001	0.68 ± 0.16 (range 0.4–1.0)	> 0.05	1.85 ± 0.43 (range 1.33–3.00)	< 0.01
contracted	20	4.11 ± 0.28	0.91 ± 0.20 (range 0.6–1.2)		0.66 ± 0.15 (range 0.3–0.9)		1.42 ± 0.36 (range 0.75–2.33)	

atic taxonomy of *Bulinus* species, where the usual planorbid chromosome number of $2n = 36$ has undergone various multiplications (Burch, 1964, 1967). Burch (1960) was the first to show tetraploidy ($2n = 72$) in a *Gyraulus* species (*G. parvus,* in the original publication misidentified as *G. circumstriatus* (Tryon) (Natarajan et al., 1965: 251)). In the present study *G. parvus* from Mainz was found to have $n = 36$ and $2n = 72$. A cytological examination of *G. laevis,* considered closely related to *G. parvus* on morphological grounds, was not possible though most desirable; animals did not survive transport to the laboratory. *G. euphraticus* from southern Iran and *G. spirillus* (Gould) from Taiwan had $n = 18$ and $2n = 36$. Burch *et al.* (1964: 221) reviewed chromosome numbers of five *Gyraulus* species, stating that in *G. tokyoensis* two of five specimens studied had 19 instead of 18 bivalents in meiotic cells; one of them even had 19 bivalents plus a univalent. Apart from chromosome numbers, the karyotype does not appear to differ between species using my techniques.

Biochemical Approaches

Biochemical data are well suited to support or disprove hypotheses about relationships between taxa including species (Davis & Lindsay, 1967; Grossu, 1977). Electrophoretic studies, for example, require living material, because samples should, whenever possible, be examined simultaneously. Since living snails were available only from a restricted number of species application of chemotaxonomic methods had to be postponed until sufficient material is successfully cultivated in the laboratory.

Parasitological Evidence

Parasitological data have been used to support or weaken conclusions about relationships to an increasing extent in several groups of animals (Fahrenholz's Rule, Eichler, 1941). Echinostomatid rediae were regularly observed during these studies, but a species identification would have required establishing life cycles in the laboratory. The expected value of the findings, however, would not have justified the expense.

Number of Eggs per Egg Mass

The number of eggs per egg mass was determined for species reared in the laboratory. Results so far seem to indicate that egg
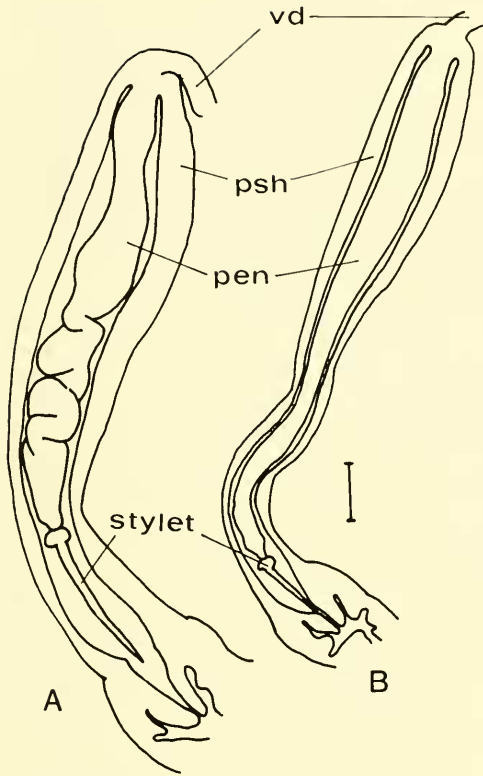
FIG. 31.   Penis sheath and penis in an individual fixed without (A) and with (B) relaxation. *G. spirillus*, Taiwan. Scale = 0.1 mm.
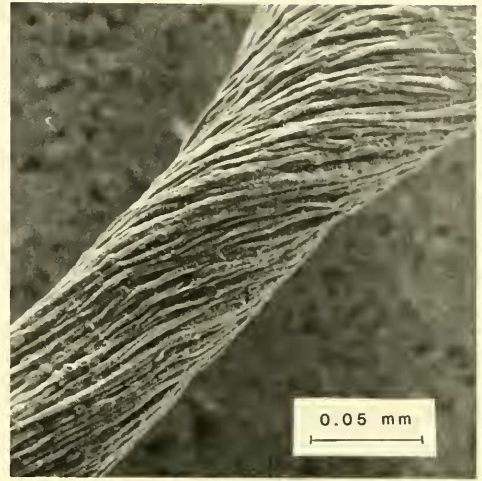

FIG. 32.   Spirally arranged longitudinal muscles of penis sheath in an unrelaxed, contracted individual, fixed in ethanol. *G. chinensis*, Chongpyong. CPD; SEM.

numbers per mass in general are correlated with snail size and are, thus, of restricted value. Nevertheless, in certain cases, when species of approximately equal sizes are compared, such as *Gyraulus albus, G. laevis,* and *G. parvus,* highly significant differences in egg numbers per mass (Table 4) are found. These support conclusions drawn anatomically. Aquarium conditions were kept constant and as similar as possible for all species: 25°C, 12 hr/12 hr light-dark regime; 2 liters of hard water (24° German hardness, $\cong 8.56$ mval/l); fortnightly water change; twisted fresh lettuce ad libitum daily; medium population density (appr. 20 to 40 mature snails in 2 liters of water).

Differences reported here between *G. albus* and *G. parvus* correspond well with those

TABLE 4.   Numbers of eggs per egg mass in *Gyraulus* species.

Species, origin, counting date	n masses counted	range	eggs/mass $\bar{x} \pm$ s.d.
albus, Zürichsee 23-IV-1974	105	1–10	6.1 ± 1.5
laevis, Haarlem 21-IX-1977	32	1–7	4.6 ± 1.2
parvus, Mainz 22-III-1974	231	1–4	2.3 ± 0.7
dto. 17-XII-1974	103	1–4	2.3 ± 0.7
dto. 30-IX-1975	140	1–5	2.4 ± 0.9
costulatus, Liberia 8-I-1975	253	2–6	4.1 ± 0.7
ehrenbergi, Cairo 7-XI-1974	119	2–8	5.0 ± 1.2
euphraticus, S Iran 19-III-1975	167	1–11	5.1 ± 2.0
chinensis, Kwekers 2-XI-1977	152	2–12	5.8 ± 1.9
spirillus, Taiwan 12-VI-1976 (density: 105 ind./2 l)	139	2–14	5.8 ± 2.2
dto., 7-X-1976 (7 ind./2 l)	88	3–14	7.4 ± 2.1

t-test: *albus/parvus, albus/laevis, parvus/laevis,* and *spirillus* high/low density $p < 0.001$.

described in the literature. Bondesen (1950: 54) even observed up to 16 eggs per mass in *G. albus,* and Krull (1931: 5), for *G. parvus* from Michigan, wrote that "masses of two or three are the most common but those of one or four are also found."

Population density greatly affects egg production as shown by data obtained at high and low densities of *Gyraulus spirillus* (Table 4). The differences between 5.8 and 7.4 are very highly significant ($p < 0.001$). Mean values of 6.1, 6.4, and 6.5 were found at intermediate densities.

Ecological Differences

Very little is known about ecological differences between *Gyraulus* species. In the case of stenotopic snails, I attach taxonomic significance to differences in physiological requirements that now probably prevent gene flow. Examples of such species are *Gyraulus rossmaessleri* with its preponderance in astatic water bodies, and *G. laevis* which appears to be favoured by a high nitrate content and often reaches high abundance in slightly brackish water. The importance of such differences in chemical and physical requirements as well as behavioural differences "in maintaining (possibly not in initiating) isolation between populations" has been pointed out for most groups of organisms (Prosser, 1974: 359). Of course, in the Planorbidae the situation is certainly not as simple as in *Paramaecium aurelia,* where Sonneborn & Dippell (1943) distinguished no fewer than 16 physiological varieties, each of which "has a potentially common gene pool which is effectively cut off from the gene pool of every other variety" and two of which are distinguished by the temperatures optimal for their growth and reproduction (Sonneborn, 1974: 173).

Although we cannot yet define the specific ecological preferences of most species, the situation in the pair of sibling species, *Gyraulus parvus* and *G. laevis* is an example of differing ecologies. My objections to the view of conspecificity of these species as represented by Jaeckel (1962: 69) initially were based on differences in ecological range, which is much wider in *G. parvus* than in *G. laevis.* As mentioned above, the latter species is both rather stenotopic and rare, while the former species is nearly ubiquitous (Clarke, 1973: 403). *G. parvus* regularly lives in pools of botanical and zoological gardens in Europe,

since 1973 constantly in a ground-water lake near Speyer (W. Germany), and in May 1977 it was collected in a forest pool near Stuttgart (S. Germany) and hence outside man-controlled water bodies in central Europe. It readily propagates in aquaria. *G. laevis,* on the other hand, is difficult to rear and is obviously diminishing in its original distribution area. These observations support the view that environmental requirements differ between the two species.

Characterization of Anatomically
Examined Species

A detailed description of taxonomically relevant organs including generic characters is given for the type-species of the genus, *Gyraulus albus.* Descriptions of other species are confined to characters of diagnostic importance. Quantifiable data are listed in tables or demonstrated in graphs as much as possible.

Before conclusions are drawn as to species delimitations, species are dealt with under provisional names. These are mostly in conformance with common use in the respective geographical areas. Type-localities are added in parentheses.

For clarity, treatment of species is subdivided according to its origin in the generally accepted zoogeographical regions ("realm") (de Lattin, 1967, fig. 87): the Palaearctic, the Oriental and, as isolated relics of Tertiary origin and foci of advanced speciation, the ancient lakes. As the borderline between Palaearctic and Orient, as found for most groups of animals, does not fit the distribution patterns in *Gyraulus* completely, chapters are headed "Europe and North Asia" and "South and East Asia."

Synonyms, even those generally accepted as correctly identified by authorities, are omitted unless I could examine preserved specimens or shells in original series, and when their identification was beyond all doubt.

Under "material" collection localities are written in short form. More detailed information on the locations is listed alphabetically in the Appendix. Spelling of names follows The Times Atlas of the World (1967) if entered there. Material preserved without relaxation and hence in a contracted state is marked "unrelaxed." All individuals without this note were relaxed and fixed, as described above. Symbols specifying material are included in parentheses.

A   angle

B   keel

C   fringe of periostr.

D   deflected last whorl

E   pilaster (d > c)

F   torus

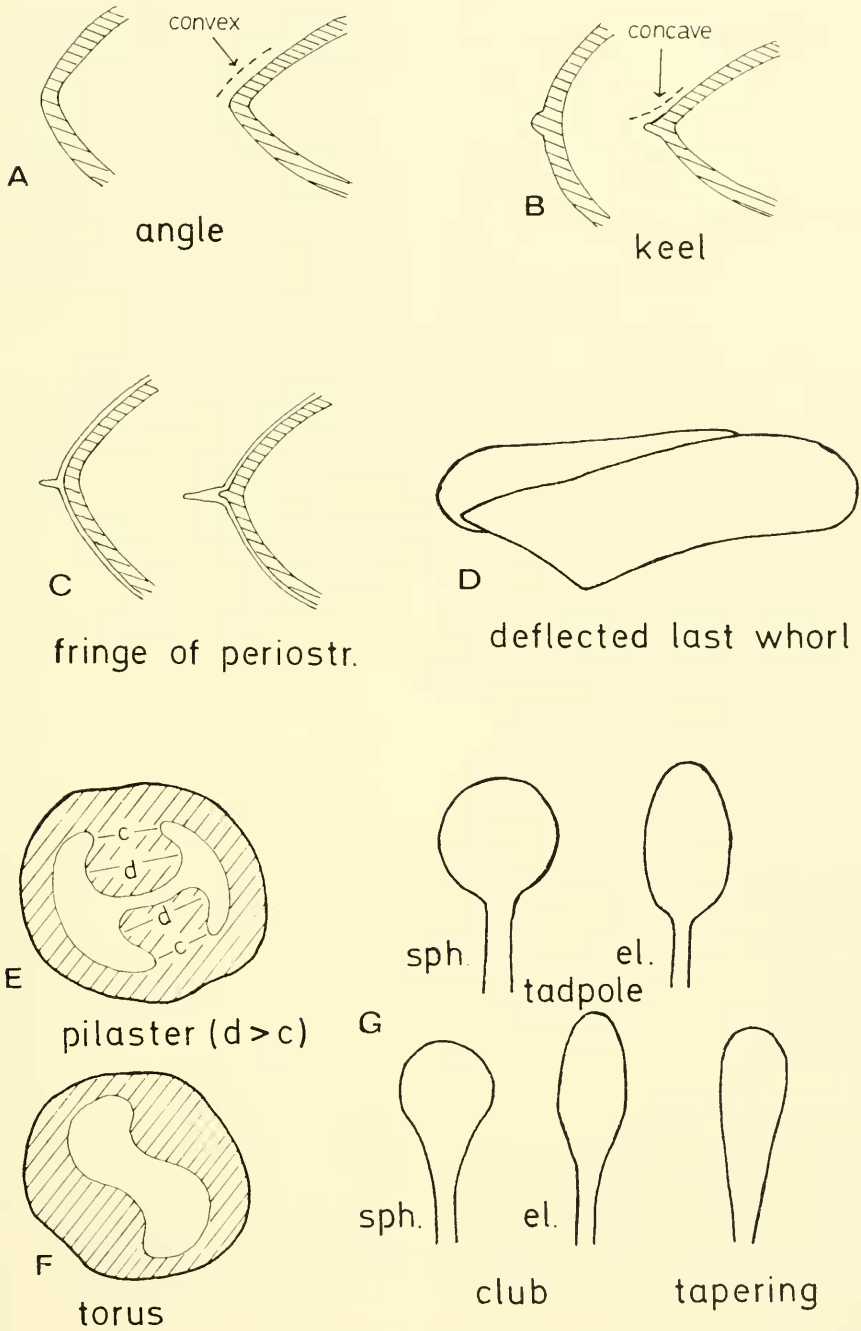G   sph.   tadpole   el.

club   tapering

FIG. 33.   Definitions. A–C: outlines of shell periphery in cross section; D: deflected last whorl (example: *G. acronicus,* Bodensee); E–F: preputial wall in cross section; G: shapes of bursa copulatrix (from top left): tadpole spherical, tadpole elongate, club spherical, club elongate, tapering.

In the figures, scales measure 1 mm unless stated otherwise. In the drawings, shaded areas indicate sectioned tissues.

MUSEUM ABBREVIATIONS

ANSP—Academy of Natural Sciences of Philadelphia

BMNH—British Museum (Natural History), London

IRSNB—Institut Royal des Sciences Naturelles de Belgique, Bruxelles

M or MG—no. in the author's collection of microsc. preparations

NHMG—Naturhistoriska Museet Göteborg

NHRMS—Naturhistoriska Riksmuseet Stockholm

MHNG—Musée d'Histoire Naturelle Genève

NMC—National Museum of Canada, Ottawa

NMV—National Museum of Victoria, Melbourne

RMNH—Rijksmuseum van Natuurlijke Historie, Leiden

SMF—Senckenberg-Museum Frankfurt/M.

ZMA—Zool. Museum Amsterdam

ZMZ—Zoologisches Museum Zürich

ZSI—Zoological Survey of India, Calcutta

DEFINITIONS AND SYNONYMOUS TERMS

The following alphabetical list of terms used here for morphological analysis, including synonymous terms, is provided to enable recognition of and the position of organs or parts of organs, and to delimit them from other organs connected or attached to them. Definitions do not include functional aspects. Terms in common and uncontroversial use in planorbid taxonomy are exempted.

angle—any interruption of a regular rounding (Fig. 33A).

club elongate (bursa copulatrix)—an elongate bursa with gradual transition to bursa duct, but not evenly tapering (Fig. 33G).

club spherical (bursa copulatrix)—a balloon-like bursa with gradual transition to bursa duct (Fig. 33G).

copulatory organ—penis + penis sheath + preputium.

deflected whorl—a whorl leaving the planispiral phase of growth toward the upper side (=under side in the sense of many previous authors, therefore: deflected = bent down) (Fig. 33D).

diaphragm—the muscular ring proximally terminating the preputium, resembling a sphincter; =velum sensu Hubendick, 1955; =Ringwulst sensu Buchner, 1891; =diaphragm or muscular ring sensu Baker, 1945.

distal—situated towards outside.

embryonic whorl—the whorl formed within the egg shell; =nuclear whorl (Fig. 10, up to arrow).

free sperm duct—the portion of the sperm duct not covered by the prostate gland.

fringe (of periostracum)—a periostracal collar on the periphery of a shell, attached to an angle or keel (Fig. 33C).

height—the maximum dimension measured perpendicular to the plane in which the whorls grow (Fig. 1).

keel—a calcareous collar on the periphery of a shell, resulting in a concave outline in cross section (Fig. 33B).

maximum diameter—measured from peristome ("outer lip") of the aperture through the innermost (nuclear) whorl (Fig. 1).

papilla—the conical to hemispherical tissue distally terminating the penis sheath, carrying a hole which is penetrated by the stylet for copulation (Fig. 29); =sarcobelum sensu Hubendick, 1955; Stilettscheide sensu Buchner, 1891; =papilla sensu Baker, 1945.

penis sheath—the proximal portion of the ♂ copulatory organ harbouring the penis, delimited proximally by the end of the vas deferens, distally by the widened lumen between papilla and diaphragm. This is the hinge-point for eversion of the preputium; =penis sac in Pan American Health Organization, 1968; =vergic sac sensu Baker, 1945; =phallotheca II auctorum (P2 Hudec, in Macha, 1963); =distale (!) Phallotheca sensu Hudec, 1967.

pilaster—a longitudinal ridge running along the inner wall of the preputium and reaching a width greater than at the site of connection with preputial wall (Fig. 33E); =muscular pillar sensu Hubendick, 1955; =Muskelpfeiler sensu Meier-Brook, 1964. (The term pilaster is preferred to pillar, because there is always a connection with the wall along its full length, whereas "pillar" implies partial detachment from the wall.)

preputium—the distal portion of the ♂ copulatory organ, delimited proximally by a weak zone between papilla and diaphragm, distally by the body integument; =phallotheca I auctorum; =proximale (!) Phallotheca or Praeputium sensu Hudec, 1967.

proximal—situated towards the inner whorls.

tadpole elongate (bursa copulatrix)—an elongate bursa with bursa duct distinctly set off (Fig. 33G).

tadpole spherical (bursa copulatrix)—a balloon-like bursa with bursa duct distinctly set off (Fig. 33G).

tapering (towards the vagina: bursa copulatrix)—a bursa evenly tapering, without a clear distinction of bursa and bursa duct (Fig. 33G).

under side—under side in a shell held with its aperture on its left side (as in apertural views of figures in the present paper); =morphological under side or conchological upper side or functional right side sensu Hubendick & Radoman, 1959; =right side sensu Pan American Health Organization, 1968.

upper side—upper side in a shell held with its aperture on its left side; =morphological upper side or conchological under side or functional left side sensu Hubendick & Radoman, 1959; =left side sensu Pan American Health Organization, 1968.

KEY TO LETTERING

agl   albumen gland
an   anus
aur   auricle
bc   bursa copulatrix
bm   buccal mass
cae   caecum
car   carrefour
cga   cerebral ganglion
dgl   digestive gland
dgld common duct of digestive gland portions
dia   diaphragm
free spd   free sperm duct
h   heart
int   intestine
intl   intestinal loop
ki   kidney
mbo   mantle border
mcol   columellar muscle
mrp   penis retractor muscle
ngl   nidamental gland
od   oviduct
oes   oesophagus
ot   ovotestis
pa   papilla
pc   pericardium
pen   penis
pgm   male genital pore

pnst   pneumostome
pp   penis pore
prp   preputium
psb   pseudobranch
psh   penis sheath
pst   prostate gland
pstd   prostate duct
rec   rectum
ret   renal tube (tubular portion of kidney)
sgl   salivary gland
ski   saccular portion of kidney
sod   spermoviduct
spd   sperm duct
st   stylet
sto   stomach
uo   external opening of ureter
ut   uterus
vag   vagina
vd   vas deferens
ventr   ventricle
vep   pulmonary vein
ver   renal vein
vs   seminal vesicle

SPECIES OF EUROPE AND NORTH ASIA

Gyraulus albus (Müller, 1774)

Planorbis albus Müller, 1774: 164, No. 350 (Fig. 34) (Fridrichsdal, Sjaelland, Denmark).

Planorbis hispidus Draparnaud, 1805.

Planorbis crosseanus Bourguignat, 1862: 42.

Gyraulus albus, Ehrmann, 1933: 170, pl. 8, fig. 104 (but not including "*G. a. acronicus* (=*Planorbis deformis* Hartmann)" listed hereunder!).

Gyraulus albus, Hubendick, 1949: 43, figs. 83–85.

Gyraulus albus, Jaeckel, 1962: 68 (but not including *G. deformis* (Hartm.) and *G. tenellus* (Hartmann)!).

P. hispidus Draparnaud was designated by Dall (1870) as the type-species of *Gyraulus.*

Material—Jorløse, Sjaelland (Denmark), 18 specs.; Switzerland: Zürichsee, 3 specs.; Greifensee, 3 specs.; Fischau (Austria), 4 specs. (unrelaxed); Germany: Kuehren, 2 specs.; Bodensee, 2 specs.; Dobersdorfer See, 2 specs.; Ettenheim, 4 specs.; Wollmatingen, 2 specs.; Ursee, 9 specs.; Windgfällweiher, 6 specs.

Shell (Fig. 35)—The shell is planispiral, of medium size (4–7 mm maximum diameter), relatively high (1.2–1.8 mm) and has 3½ (at most 4 or 4¼) whorls, which rapidly increase

350. PLANORBIS albus.

Planorbis testa alba, utrinque umbilicata, aper-
tura dilatata.

Planorbis minima duorum orbium. Petiv. gazophyl.
t. 92. f. 7.

Berl. Magaz. 4. B. p. 253. t. 8. f. 23.

Dan. den hvide skive.

diam. 1 - 2 lin. alt. 1 lin.

Testa albida, pellucida, raro subfusca, supra planiuscula, sub-
tus convexa, utrinque æque umbilicata. Anfractus teretes, in
adultis ad summum quatuor; lenticulæ oculari striis longitudinali-
bus & transversalibus insigniti, hæ in quibusdam obsoletæ & vix
detegendæ, illæ satis conspicuæ. Anfractus extimus reliquis omni-
bus major & latior, superna ejus pars ultra infernam valde exten-
sa est, uti in P. Purpura. Apertura rotundata, larga, obliqua
margine inferiore anfractum vicinum tegit.

Linax griseus, 1½ lin. longus. Tentacula albida ejusdem
fere longitudinis. Soli oculi nigri.

Vasculo vitreo servati copula medio Julii jungebantur, simul
agentes & patientes. Membra genitalia latere sinistro.

In plantis aquaticis amnis Fridrichsdalensis.

FIG. 34. Facsimile of O. F. Müller's description of
Planorbis albus (1774: 164).

FIG. 35. *G. albus,* Sjaelland. Shell shape: A—lat-
eral view, B—upper side, C—apertural view, D—
under side (SMF 246 302).

in width. The last whorl expands towards the
aperture and ends in a broadening bend. The
whorls are a little wider than high, giving the
aperture an ovoid shape. Each whorl scarce-
ly embraces the preceding one; the whorls
are equally rounded on each side as well as
peripherally and rarely have a trace of an an-
gle. The shell is slightly concave on the under
side and deeply concave on the upper side.
The last whorl is not or very little deflected.

Growth lines are arcuate, crossed by spiral
striae, both forming a reticulate surface
sculpture (Fig. 36A, B). This sculpture is usu-
ally well developed; when weakly developed
it is visible at least on the upper side of the
shell. The surface is never glossy; the peri-
ostracum sometimes has short hair-like pro-
trusions; these are part of the periostracal
ridges formed on growth lines, the ridges
being stretched out to triangular laminae on
the nodules formed at the crossing points.
"Hairs" thus follow the spiral striae (Fig. 36C).
The color is light-corneous.

Animal (Fig. 37)—The animal is light to me-
dium grey. The pigment is distributed not quite
evenly on the cephalopedal mass that com-
prises body portions extended out of the shell
during crawling. The tentacles are lighter, ex-
cept for a central line that is darker; pigmen-
tation is cloudy on the remaining parts. The
anterior mantle roof (Figs. 11 and 37) is dif-
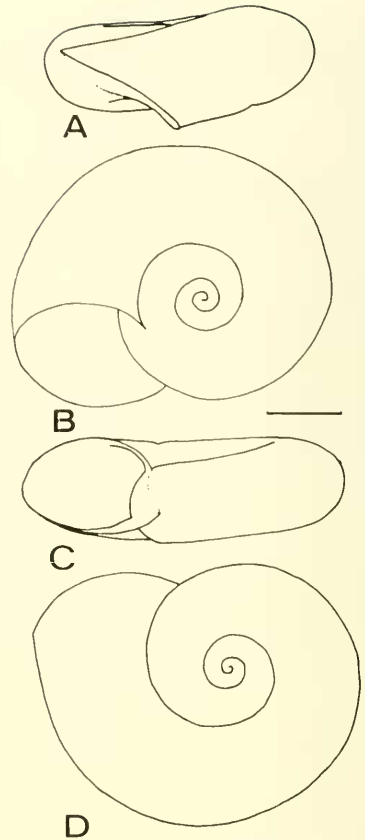fusely pigmented, showing a cloudy pattern.

The mantle roof is dark grey on the right side,
in a zone parallel to the columellar muscle.
Pigmentation is weaker and diffuse to almost
absent in between this densely pigmented
zone and the peripheral region. At the periph-
ery there is a narrow longitudinal unpigment-
ed stripe indicating the position of the pul-
monary vein (Fig. 37A, vep); next to it the
kidney roof is densely pigmented. The renal
vein (Fig. 37A, ver), again devoid of pigment,
delimits the kidney on its left side. The re-
maining portion of the left mantle side is
weakly pigmented, only a few scattered pig-
ment cells being present.

Pallial Organs (Fig. 38)—The pallial cavity
extends back from the thickened mantle bor-
der (mbo) to about ⅔ of the last whorl. The
dorsal part of the mantle roof is occupied by
the kidney. The kidney consists of the very

short saccular portion (ski) situated to the left of the pericardium (in dorsal view) and the long renal tube (ret). Anteriorly, the kidney tapers off and ends in a reflected ureter, discharging (uo) behind the pneumostome (pnst). In extended individuals the kidney has straight margins; there are no septa in the lumen of the renal tube. None of the three pallial ridges regularly found in other planorbid groups is developed.

The mantle border is partially connected with the roof of the cephalopedal mass by connective tissue (Fig. 39). The pallial cavity opens on the left side through the pneumostome (pnst) formed by the mantle lobe, which in the living snail is held against the mantle border (mbo), together with the pseudobranch (psb). The pseudobranch is triangular to rectangular and carries a longitudinal fold. The rectum ends (an) near the base of the pseudobranch on the right of this fold.

Alimentary Tract—The jaw is composed of numerous chitinized bars, approximately 12 in the median part, and 15 to 20 in each of the lateral portions (Fig. 40).

The radula of a sexually mature animal consists of approximately 150 transverse rows of teeth. The almost straight rows are formed by 27 to 35 single teeth (Fig. 41); the central tooth is bicuspid (Fig. 17). A small additional denticle regularly occurs between the cusps; similar denticles are found on both sides of the tooth, but nearer to the base. The base broadens posteriorly. The lateral teeth are tricuspid. The mesocone is the longest one; the endocone is a little shorter and the ectocone the shortest. Again there are additional denticles between each cusp and on both sides of a tooth. The base of the lateral teeth has parallel edges directed obliquely towards the lateral posterior region of the radula. About the 10th or 11th lateral tooth shows the first signs of a conversion to marginal teeth. These are pluricuspid, but the three cusps of the lateral teeth, particularly the mesocone, are still pronounced, though narrower. The denticles increase in number and size (Fig. 42). Cusps and denticles together total a dozen or even more. Variation of radula characters is slight.

The oesophagus emerges from the dorsal part of the buccal mass and penetrates the ring of the central nervous system as a narrow tube. A short distance behind the central nervous system it widens abruptly and runs backwards along the right side of the body,
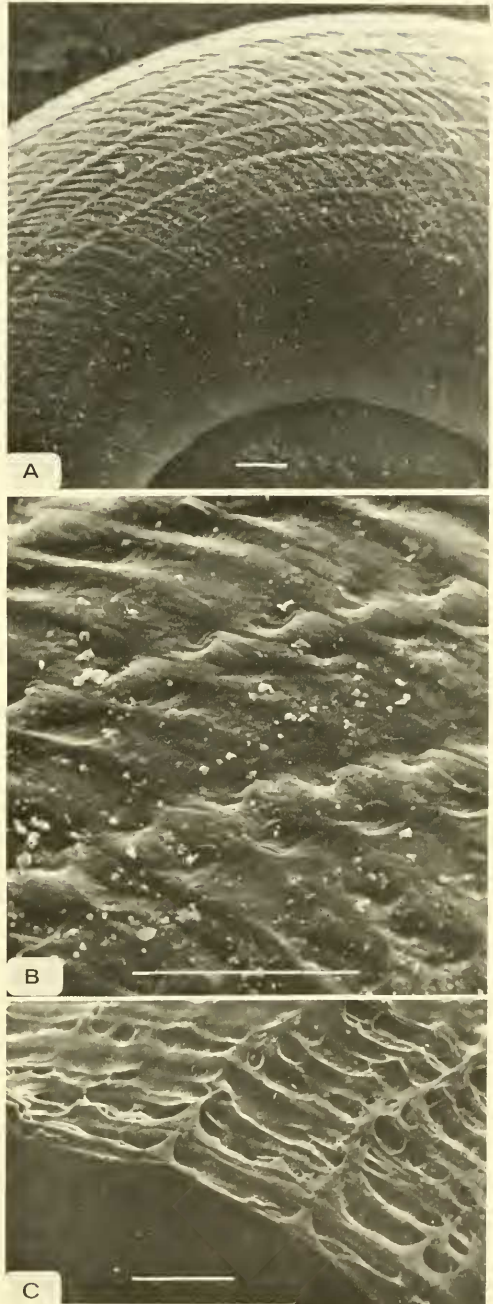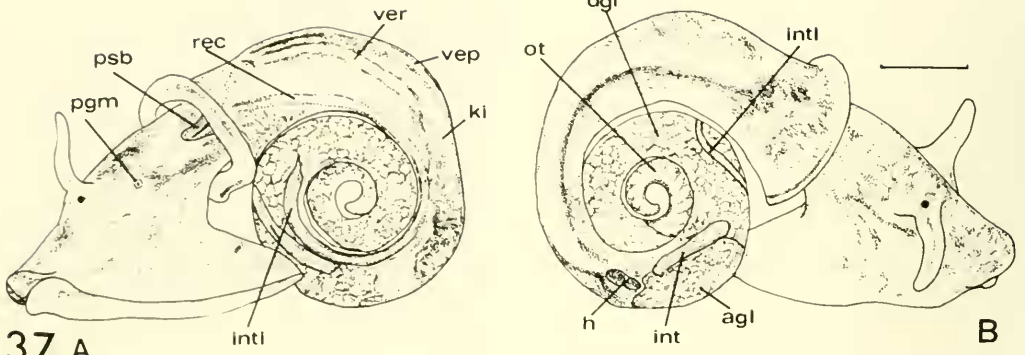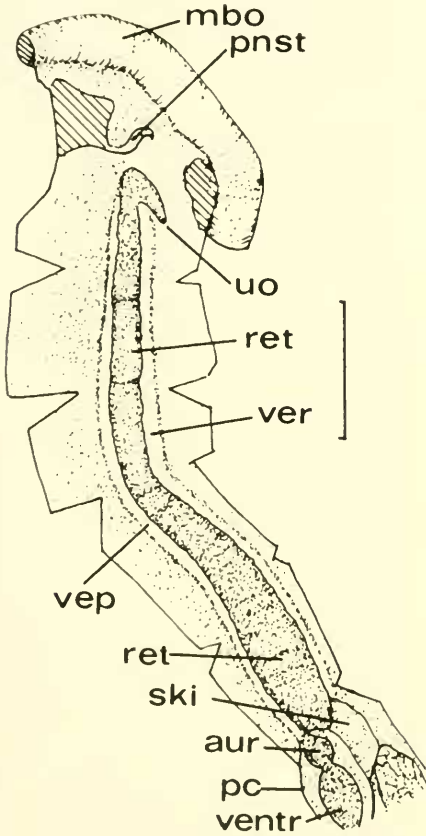

FIG. 36. Shell surface of *G. albus*, Sjaelland, with characteristic reticulate sculpture (A, B) or "hairs" (C). Scales = 0.1 mm.
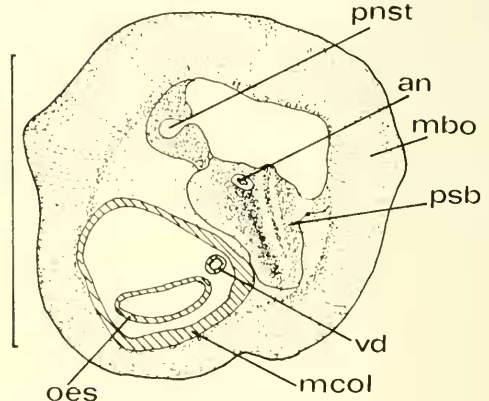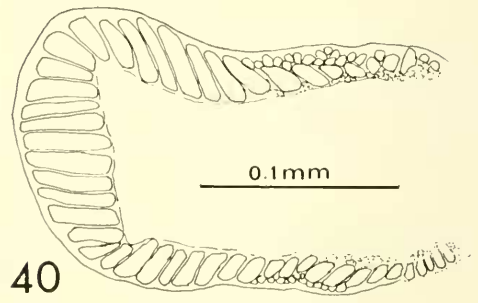
FIGS. 37–40. *G. albus*, Sjaelland. 37. Animal with shell removed, viewed from the left and right, to show pigmentation and position of organs visible externally. 38. Ceiling of mantle cavity showing kidney region. Ventral view (SMF 246 301). 39. Mantle border in frontal view. Cephalopedal mass and portion behind mantle border cut off. Relaxed individual with widely dilated pallial opening. 40. Jaw (M 289).

usually attached to the exterior side of the prostate gland. Behind the end of the pallial cavity it turns to the middle and widens, forming a crop. This leads to the strong mus-cular part of the stomach (the gizzard) that is always filled with sand grains.

The intestine leaves the stomach on its right posterior side and bends anteriorly (Fig. 18).
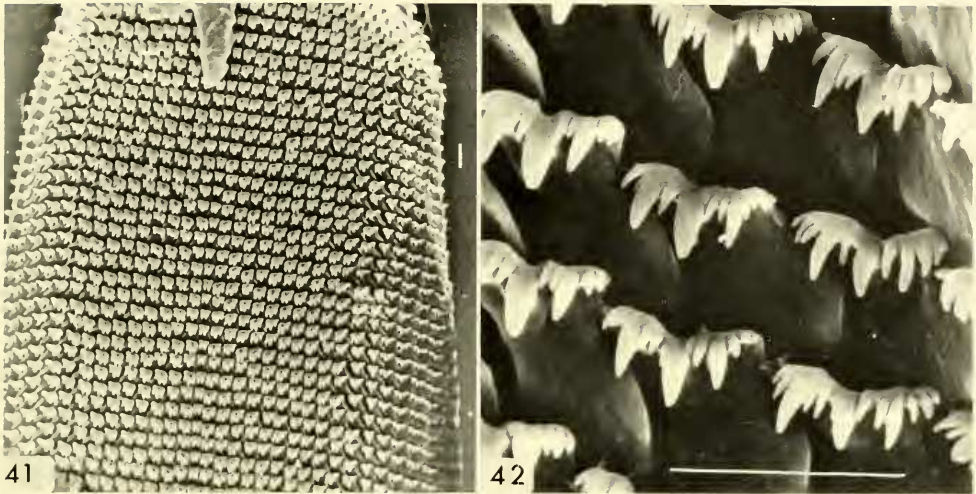
FIGS. 41–42.   *G. albus,* Sjaelland. 41. Transverse rows of radular teeth. SEM. Scale = 0.01 mm. 42. Marginal teeth nos. 13–15. SEM. Scale = 0.01 mm.

At the bending point the short duct of the digestive gland merges into the intestine. A caecum, in the anteriad direction, follows immediately. The intestine then follows the course described above as an intestinal loop (Fig. 18). The rectum makes its way to the pseudobranch on the extreme left side of the floor of the pallial cavity.

The salivary glands insert on the dorsal part of the buccal mass, close to the oesophagus. They penetrate the nerve ring together with the oesophagus, buccal retractor muscles and cephalic arteries. The two unequal parts of the digestive gland (Fig. 37B, dgl) almost fill the whole space from the central part of the stomach to the middle of the ovotestis. Only the intestinal loop and the spermoviduct with the seminal vesicle are embedded in it.

The intestinal loop may be more or less well developed, i.e. longer or shorter. Complete lack of the loop has not been observed in *Gyraulus albus.*

Reproductive System (Fig. 43)—The ovotestis (ot) consists of a double row of 20 to 30 lobes. The anterior part of the ovotestis is situated on the left side of the posterior end of the digestive gland. The spermoviduct (sod) is embedded ventrally in the middle of the latter. It leaves the ovotestis as an initially wide and delicate tube, then narrowing and, after a short distance, coiling up to form the seminal vesicle (vs), where sperm is stored after production. A narrow distal part, considerably longer than the proximal one, follows and

enters the rather voluminous carrefour (car). This is a complex hollow organ, entered also by the tiny duct of the albumen gland (agl). The albumen gland is a compact organ, convex dorsally, concave ventrally, composed of numerous small acini.

Distal to the carrefour the female and the male tracts of the reproductive system separate. The oviduct leaves the carrefour on the left side as a wide and irregularly shaped tube.
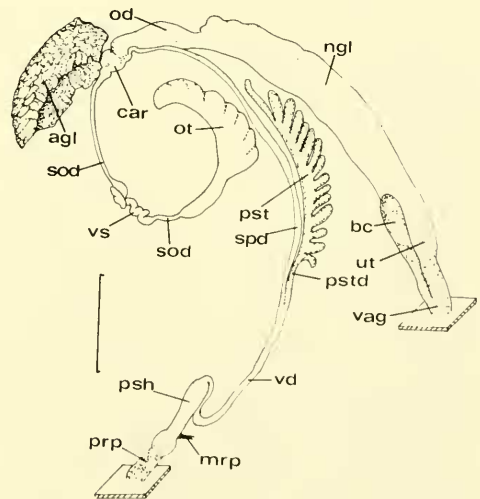

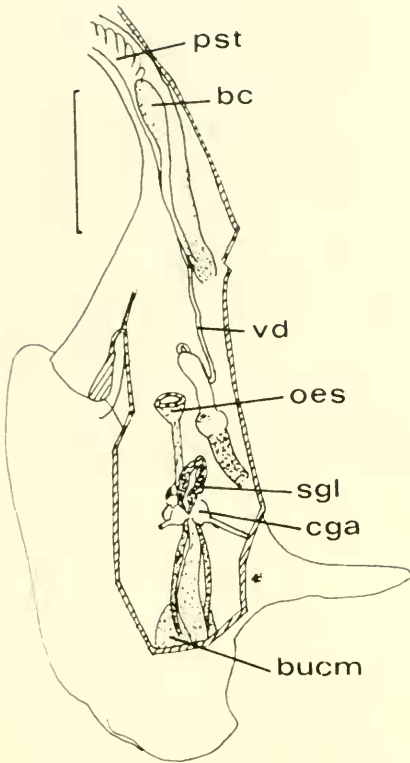FIG. 43.   Reproductive system of *G. albus,* Sjaelland. Max. shell diameter 5 mm, 4¼ whorls (M 286). Key to lettering p. 27.

FIG. 44. Position of distal genitalia in a fully extended *G. albus*, Sjaelland. Roof of cephalopedal mass and posterior portion of oesophagus removed (SMF 246 301). Key to lettering p. 27.

Its transition to the part joined by the nidamental gland is mostly invisible from the outside. Under favourable circumstances the nidamental gland can be distinguished from the oviduct by its opaque yellowish appearance. The uterus can be told from the nidamental gland by a more transparent and colorless appearance. The uterus finally narrows abruptly towards the vagina, which is uninflated or, at most, weakly inflated near the ♀ genital pore. Here the bursa copulatrix branches off with a duct of moderate width. The bursa is club-shaped in *Gyraulus albus*, usually elongate, rarely more spherical. It is always narrower than the uterus.

The male tract emerges from the carrefour on the right ventral side. The sperm duct is always considerably narrower than any part of the female tract. It lies close to the oviduct and is joined by the duct of the prostrate gland. Their fusion takes place gradually so

that it cannot be clearly located in many cases. The prostate duct is longer than half the sperm duct. A number of diverticula merges into the duct. These are densely arranged in a single row and are not separable histologically from the prostate duct. Diverticula are unbranched in the vast majority of examined individuals; the bifid condition rarely occurs. A more scattered, irregular and less dense arrangement of diverticula was observed in several individuals of one population (Sjaelland, Denmark). Numbers of prostate diverticula usually vary from 13 to 20. In one population, numbers as low as 7 were counted (Table 1).

The vas deferens, extending between the point of fusion of the prostate duct with the sperm duct and the ♂ copulatory organ, is relatively wide.

The ♂ copulatory organ is comparatively short. In relaxed and well extended animals of *Gyraulus albus* its proximal end at most reaches up to the bursa copulatrix, but often not even to the vagina (Fig. 44). The penis sheath (psh) is 1.5 to 2.0 times the length of the preputium (Table 2). It is club-shaped in outline, being narrowest near its middle. A knob-like thickening of the copulatory organ in the region of the papilla and diaphragm indicates the border between the two portions in external view. A single retractor muscle inserts at the penis sheath near its distal end.

The preputium has relatively thin walls that are folded inwards, but too little to form pilasters (see definitions). The preputial lumen is oval in cross section or slightly S-shaped. The male copulatory organ opens outwards a short distance behind the left tentacle (Fig. 37A, pgm).

The penis is enclosed in the penis sheath. It consists of a long tube, uniform except at its tip. Distally the penis is thickened on one side (see Meier-Brook, 1964, figs. 25, 28). The orifice of the sperm canal (pp) is in the distal half of the thickening, and is often subterminal. Variation in the form of the penis tip and position of the penis pore, is moderate (Fig. 45). The groove between the penis pore and the opening of the stylet is wide and shallow, not narrow as shown for *Gyraulus euphraticus* (Fig. 28). The stylet varies a little in size and shape, but is generally similar to that figured from other species (Figs. 25–28).

As to the histology of the ♂ copulatory organ, I refer to the excellent account by Buchner (1891: 78–84, pl. V: 1) for *Anisus vortex*.

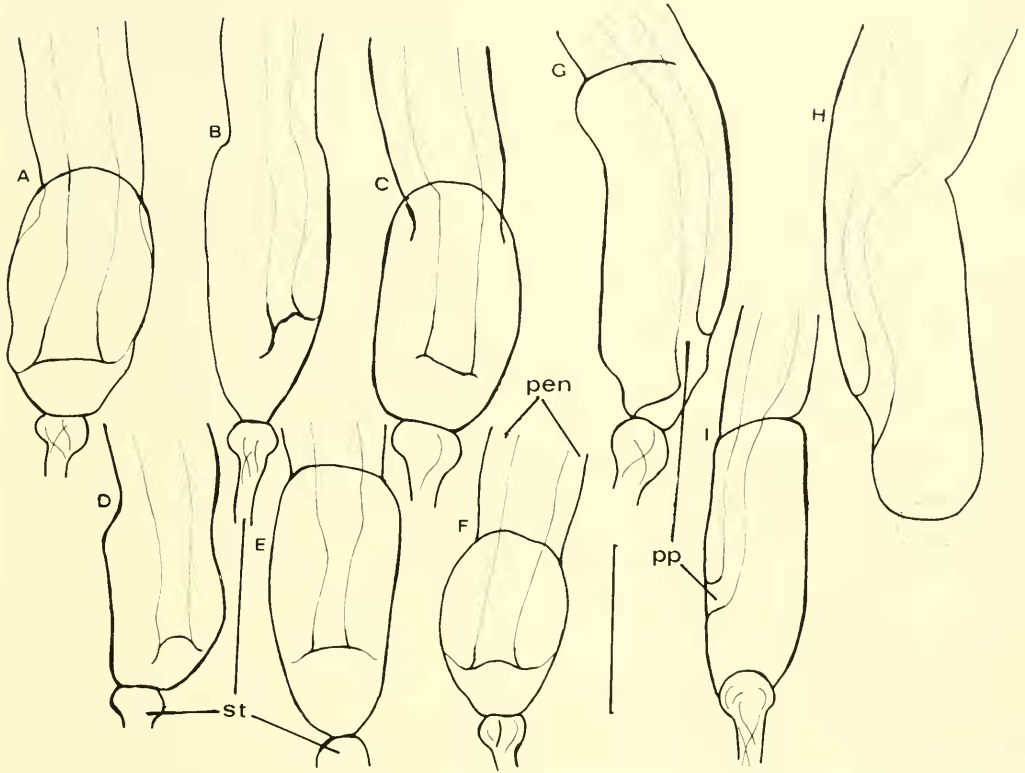Remarks—*Gyraulus albus* is so well sep-

FIG. 45.   Variation in shape of penis tip and position of penis pore in *G. albus*. A–F: Sjaelland (M 286); G–H: Ettenheim (M 288); I: Kuehren (M 90). Scale = 0.1 mm.

arated from any other species of the genus that problems arise neither in delimitation nor in recognition. Shell characters alone are sufficient to distinguish this species from others. *G. albus* is distributed all over Europe; it is most frequent in temperate climates. It extends far to the east. Khazannikov (1973: fig. 1) figured ♂ copulatory organs clearly proving correct identification of this species from the River Terek Basin (northeast of the Caucasus), but so far this is the most eastern record of anatomically-identified specimens. All records from Central or East Asia seem to have been published by authors who only knew *G. albus* from descriptions and insufficient illustrations, or had little experience with this species. Thus, the species named *Anisus (Gyraulus) albus* by Mori (1938: 294, pl. 16: 13) was doubtlessly misidentified, as judged from the description and figures. Kuroda's listing of *G. albus* (1963: 23) and of *G. spirillus* as one of its synonyms was evidently based on Mori's paper. Consequently

it is highly probable that this species does not live in Japan.

Yen (1939: 69) claimed that *Gyraulus albus* was frequently found in N and S China. I examined the material in the Senckenberg-Museum, Frankfurt. The shells in the three lots named *G. albus* from Sagsagyr/Ordos, Peak/Hongkong and Pok-Fulam/Hongkong (Yen, 1939, pl. 6, fig. 6) are devoid of any spiral striation and cannot be distinguished from the material anatomically examined and identified as *G. chinensis* in this study.

It must be conceded, however, that at that time—and until recently (Jaeckel, 1962: 68)—*Planorbis deformis* Hartmann was considered a variety of *Gyraulus albus*, and that in E Asia there are indeed snails resembling *P. deformis* at first glance. *P. deformis* has, in the meantime, proven to be a synonym of *G. acronicus* (Meier-Brook, 1964). Whether *G. albus* is conspecific with North American forms such as *G. deflectus* (Say, 1824) and *G. hirsutus* (Gould, 1839) cannot yet be an-
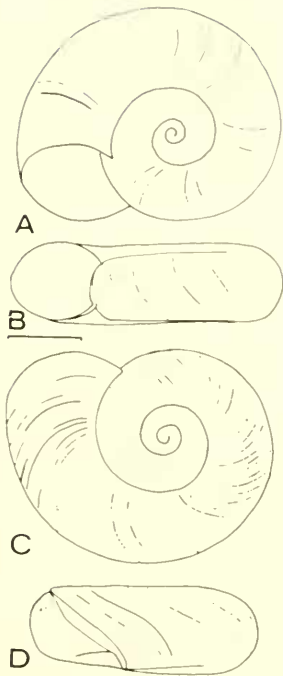
FIG. 46.   *G. laevis*, Kuehren. Shell. A—upper side,
B—apertural view, C—under side, D—lateral view
(SMF 246 308).

swered satisfactorily. Species identity of these
has been claimed by Dall (1905) and Baker
(1928), but other authors have questioned this
on conchological grounds (Miller, 1966;
Clarke, 1973). Judging by Baker's (1945: pls.
15, 16) anatomical figures, the two American
species have a ♂ copulatory organ at least
twice the length of that of *G. albus*.

Gyraulus laevis (Alder, 1838)

Planorbis laevis Alder, 1838: 337 (Whitley
    Quarries near Newcastle).
Planorbis thermalis Westerlund, 1885: 83
    (Bad Villach).
Gyraulus laevis, Ehrmann, 1933: 170, pl. 8,
    fig. 105.
Gyraulus laevis, Jaeckel, 1962: 69.

Material—Kuehren (Germany, 16 specs.,
including 5 trematode-infected ones with
underdeveloped reproductive organs; Haar-
lem (Netherlands), 12 specs.; Bad Villach
(Austria), 10 specs. (*Gyraulus thermalis*).

Shell (Fig. 46)—The shell is a little smaller
than in *Gyraulus albus* (4 mm maximum di-
ameter), relatively high (1.3 mm); it has 3½
whorls, which increase regularly in width, the
last one not expanding towards the aperture.
The whorls are scarcely wider than high and
separated by deep sutures; the aperture is
roundish. The periphery is rounded, never
keeled or angled. The shell is deeply concave
on the upper side; on the under side, the
whorls interior to the penultimate one are also
concave; the whorls are more rounded on the
under side than on the upper side. Growth
lines are less arcuate than in *G. albus* and
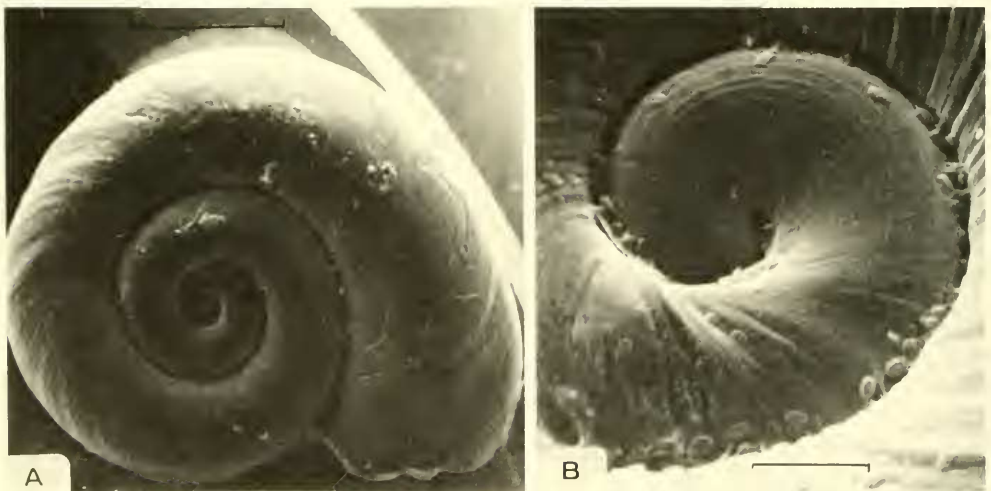irregular. The surface is smooth (Fig. 47) and

FIG. 47.   *G. laevis*, Kuehren. Shell surface, SEM. A—whole shell. B—spiral striation on embryonic whorl.
Scale = 0.1 mm.
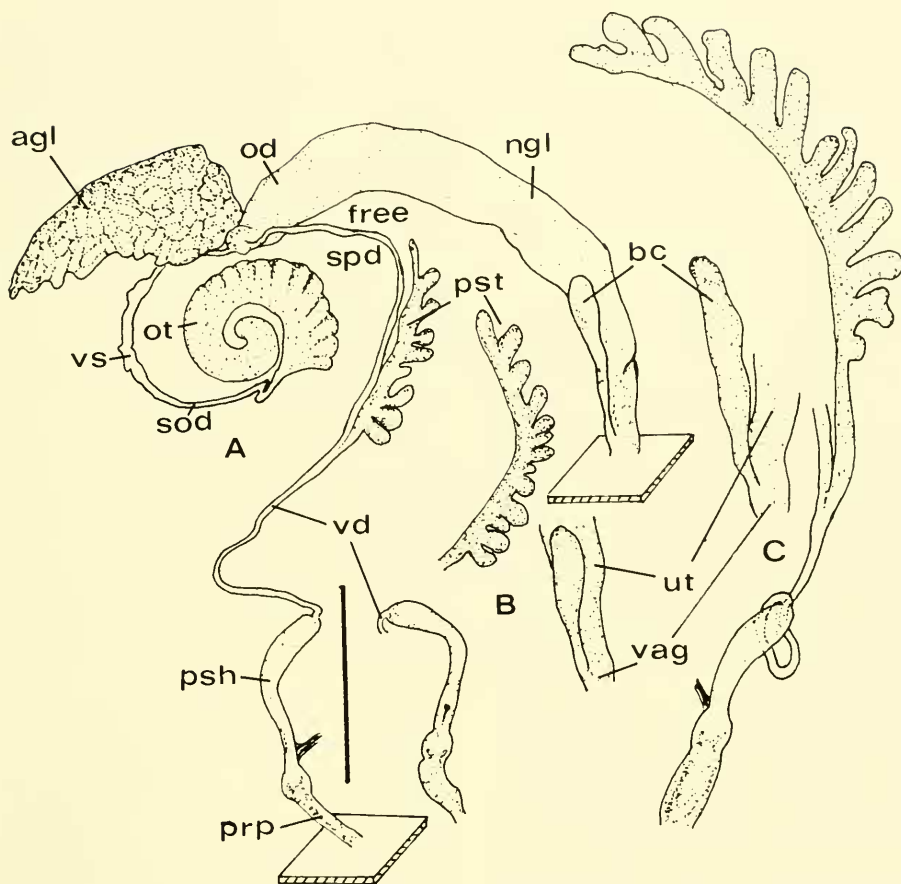
FIG. 48. *G. laevis,* Kuehren. Reproductive system. Maximum shell diameter: A—3.4 mm (SMF 246 309), B—3.6 mm (M 290), C—5.4 mm (M 66). Key to lettering p. 27.

slightly glossy; spiral striae are absent except on the nuclear whorl, as in all species. The color is brownish.

In the population at Bad Villach named *Gyraulus thermalis* shells are smaller, 2 to 3 mm in diameter, 0.9 to 1.0 mm in height, with 3 to 3¼ whorls.

Animal—The animal is moderately grey and scarcely pigmented; the mantle roof is virtually unpigmented except on the kidney and lateral borders of the accompanying veins where scattered pigment cells are found. The mantle border is unpigmented. The extreme right portion of the mantle covering the reproductive tract is more densely pigmented. Conspicuously dark pigmentation is present only in the heart, stomach and intestine between stomach and flexion (Fig. 19, arrow).

There are several distinct septa in the kidney giving it an undulate shape (Fig. 14). The jaw and radula are not fundamentally different from those described for *Gyraulus albus*. An intestinal loop was lacking (Fig. 19) in ten individuals and well developed in six from the population at Kuehren.

In the reproductive system (Fig. 48), the distal portion of the spermoviduct is wider (0.030–0.033 mm) than the two halves of the vas deferens in their respective middle parts (proximal half ~ 0.012 mm; distal half ~ 0.018 mm) and also wider than the sperm duct. The bursa copulatrix is inconspicuous, elongate club-shaped or tapering. The prostate gland is so delicate that it is almost impossible to detach it from the female tract without damage. It shows two unusual features: the scattered arrangement of diverticula and their changing shape. The number of

diverticula seems to be slightly less than in *Gyraulus albus* (Table 2). The vas deferens is similarly narrow in both halves (see above). The δ copulatory organ is not longer than that in *G. albus* (Table 2). Microphally was observed in trematode-infected individuals (x̄ = 0.60 ± 0.2 mm). The length ratio penis sheath : preputium is also similar to that in *G. albus*. The preputium cannot be distinguished from that of *G. albus*.

The penis shows considerable variation in shape. In larger individuals (e.g. Fig. 48C) it is nearly congruent with those figured for *Gyraulus albus* in Fig. 45E and similar forms. In smaller individuals 3.3–4.0 mm in diameter, the distal thickening is regularly undeveloped; the tip is rather conical in shape, and the penis pore is lateral rather than subterminal. This shape and penis pore position is possibly a sign of immaturity although an orange color in all individuals indicates that copulation has taken place. The question deserves further attention. Smaller individuals with an incompletely differentiated stylet and a colorless bursa copulatrix have been exempted from evaluation.

Remarks—*Gyraulus laevis* has been defined as a distinct species conchologically for a long time. Doubts can arise, where *G. laevis* and *G. albus* occur together and the latter has weak spiral striation. However, the septate kidney and the irregular prostate diverticula provide good characters for safe distinction. *G. laevis* is closely related, though not identical, with the North American *G. parvus*, which is included here for comparison and because it lives on Iceland and has been introduced to Europe. The only anatomical description of *G. laevis* thus far published is by Soós (1935: 26, fig. 3). From his figure it can be seen that his Hungarian material resembles that presented here in the irregular prostate diverticula, their number (11), the short δ copulatory organ, and the club-shaped bursa copulatrix. Soós, however, expressed the opinion that *G. laevis* differs anatomically from *G. albus* only to a negligible degree.

Gyraulus thermalis has been given the rank of a subspecies of *G. laevis* or a species endemic to the thermal spring of Villach (Klemm, 1960: 12; Jaeckel, 1962: 69; Jaeckel, 1967: 103). However, the small size of *G. thermalis* appears to be the only character by which it constantly differs from *G. laevis*. In this connection it may be noted that there are more instances in the genus where thermal springs harbor snails significantly smaller than those that occur in cooler waters. One is *G. acronicus* from Paratunka (Kamchatka): the snails were collected "near hot springs"; the biggest of 97 individuals was 4.7 mm in diameter, whereas samples from other Siberian localities contained snails exceeding 6 or 6.5 mm in diameter. The other example is *G. parvus* from a warm spring in Iceland (about 30°C, as estimated by the collector). Snails from two shipments were transferred to aquaria at 25°C in attempts to raise larger individuals for anatomical studies. They all died before growing larger than 2.5–3.0 mm diameter. As the sample also never contained empty shells larger than these, I assume that they do not exceed this size in their natural habitat. The mechanism causing dwarfism in warm springs is not yet understood. At any rate it is unlikely that a process of speciation has been initiated here. Only in such a case would it be justified to raise a dwarf form, such as *thermalis*, to subspecies rank. Experimental analysis should clear up how far in phenotypical dwarfism genetically fixed characters are involved. It seems preferable to deal with *thermalis* as merely an ecological form.

Snails diagnosed as *Gyraulus laevis* have been recorded from Europe and Asia as far east as Kamchatka. According to Alzona (1971) the species is said to live all over Italy, and other records were published on its distribution in other Mediterranean countries, sometimes under names such as *G. agraulus* and *G. numidicus*. In one case an anatomical figure was published of "*Gyraulus agraulus.*" This figure clearly proves that the material does not belong in *Gyraulus* (Giusti, 1968).

In attempts to obtain more material of *Gy-*

→

FIGS. 49–52. *G. parvus.* 49. Ann Arbor (U.S.A.). Shell (SMF 246 310). A—upper side; B—apertural view; C—under side. 50. Variation in prostate glands. A, B: Ann Arbor (M 30), C: W Iceland (M 198), D: SE Iceland (MG 208). 51. δ copulatory organ (Speyer) and characteristic vas deferens being wide in the distal half (0.050 mm in its middle) and narrow in the proximal half (0.018 mm) (M 227). Scale = 0.1 mm. 52. Variation in shape of penis tips and position of penis pore. A, B: Ann Arbor (M 81, 83); C, D: W Iceland (M 199); E, F: SE Iceland (M 274); G, H: Speyer (M 275). Scale = 0.1 mm.
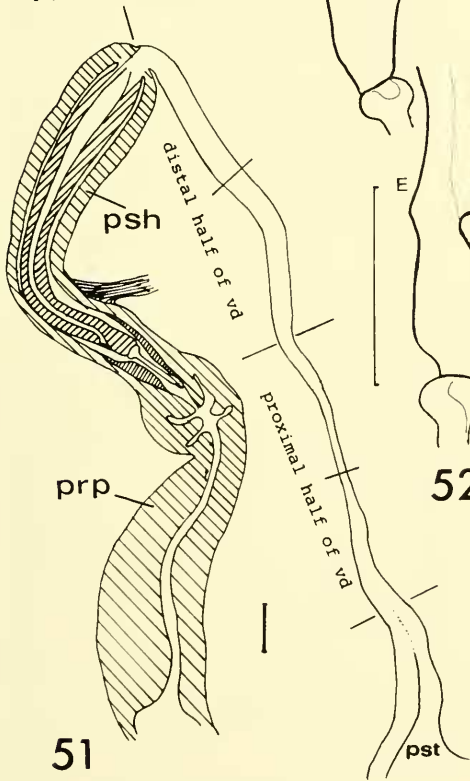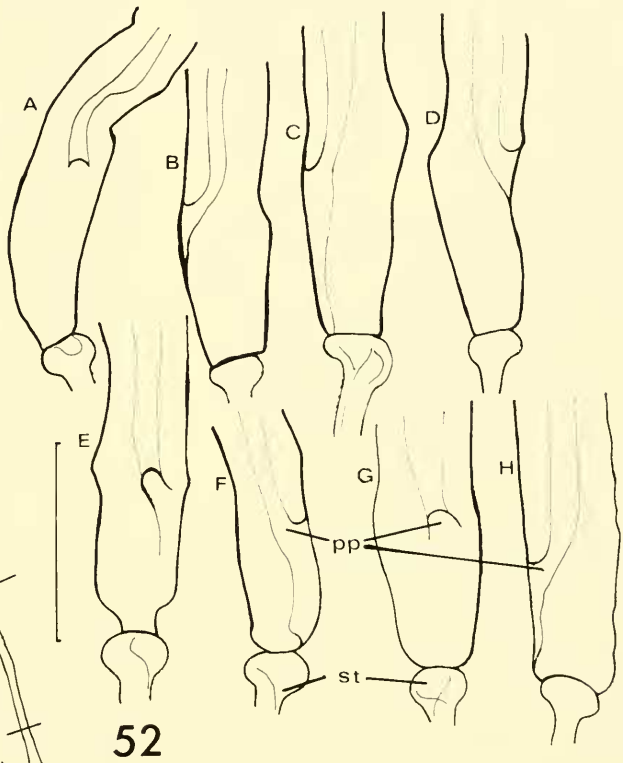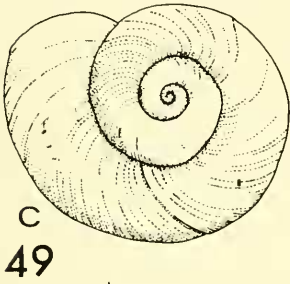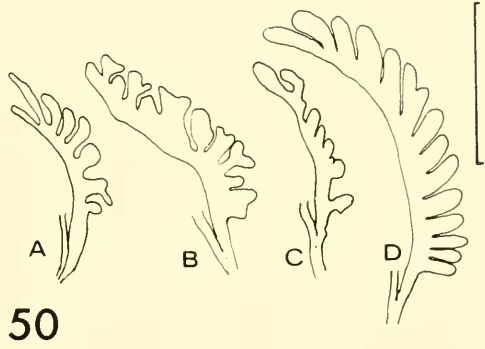
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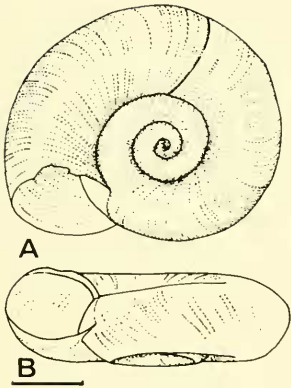
TABLE 5. Reproductive organs of *Gyraulus parvus*.

Locality	No. prost. divert.			Male copulatory organ						Bursa copul.		
				Total length (mm)			Ratio psh:prp			clb. el.	clb. sph.	tap.
	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.			
Ann Arbor	5	7–10	8.5 ± 1.1	6	1.1–1.6	1.4 ± 0.2	1.1–2.5	1.6 ± 0.6	+	+	+
Abitibi-R¹				3	0.8 + 0.8 + 1.2		1.5 + 1.7 + 2.3			+	+
Lesser Slave L.¹	2	10 + 12		2	1.4 + 1.8		1.6 + 1.0			+	+
W Iceland	4	6–9	8.0	4	1.0–1.3	1.1	1.9–2.3	2.1	+		+
SE Iceland	5	12–14	12.8	7	1.2–1.6	1.5 ± 0.1	1.5–2.5	2.0 ± 0.3	+		+
Mainz	9	9–17	12.1 ± 2.9	8	0.9–1.7	1.2 ± 0.2	1.3–2.3	1.8 ± 0.3	+		+
Speyer	6	10–16	12.2 ± 2.0	7	1.3–2.0	1.6 ± 0.2	1.2–2.0	1.5 ± 0.3	+		+
Total	31	7–17	11.0 ± 2.7	32²	0.8–2.0	1.4 ± 0.2	1.1–2.5	1.8 ± 0.4			

¹ Unrelaxed.
² Excl. unrelaxed individuals from Canada.

raulus laevis, I have dissected snails identified as *G. laevis.* Moreover, I checked drawings of material studied and kindly provided by Dr. Giusti from various Mediterranean islands. Specimens from Crete, Corfu, Rhodos, Elba, Montecristo, Corsica, Sardinia, Mallorca and, moreover, from Madeira had anatomical features of the genus *Planorbis*; it is therefore doubted that *G. laevis* lives in the Mediterranean region. The occurrence of this species in Asia must also be doubted unless anatomical evidence proves the contrary.

Gyraulus parvus (Say, 1817)

Planorbis parvus Say, 1817: pl. 1, fig. 5 (Delaware River, near Philadelphia).

Material—Ann Arbor (U.S.A.), 13 specs.; Abitibi River (Canada), 3 specs. (unrelaxed); Lesser Slave Lake (Canada), 2 specs. (unrelaxed); W Iceland, 5 specs.; SE Iceland, 3 specs.; Germany (introduced): Speyer, 11 specs.; Mainz, 11 specs.

Shell—The shell is small, deeply umbilicate on the upper side; on the under side the penultimate whorl is strikingly elevated (Fig. 49). Both the inner whorls and the last whorl are sunken or deflected respectively. This character state is more strongly developed in *Gyraulus parvus* than in *G. laevis*. The whorls are rounded or nearly angled on the under side; the sutures are deep. The surface is smooth and glossy; no spiral striation is present. The color is light-corneous to brownish.

Animal—The animal is very weakly pigmented, like *Gyraulus laevis*. The kidney has distinctly undulate margins. The intestinal loop was lacking in all individuals seen. The seminal vesicle is inconspicuous to slightly bulbous; the distal portion of the spermoviduct is as narrow as in *G. albus.* The vagina is not or scarcely inflated. The bursa copulatrix is as narrow (and relatively long) as in *G. laevis,* mostly tapering or elongate club-shaped, rarely spherical club-shaped. The number of prostate diverticula is insignificantly less than in *G. laevis* (Table 5). The shape of the diverticula is still more irregular than in *G. laevis* (Fig. 50A–C), often branched, but in two populations (SE Iceland, Speyer), regularly and closely spaced diverticula occasionally occurred (Fig. 50D). The most consistent character state in *G. parvus* is the strikingly changing width of the vas deferens (Fig. 51). In its course it narrows in between as usual

in most species, but in its distal half it widens so much that its diameter becomes twice that of the proximal half (width ratio distal : proximal half: $\bar{x} = 2.1 \pm 0.5$, range 1.3–3; n = 22).

The ♂ copulatory organ is similar to that of *Gyraulus laevis*; its total length as well as proportions are of the same order of magnitude. The preputium does not have pilasters, but its lumen is S-shaped. The penis, in most cases, has a slight terminal thickening (Fig. 52A–E), less distinct than that shown for *G. albus* (Fig. 45), but incidentally such a thickening may be indiscernible (Fig. 52F, H). The penis pore lies within the terminal thickening or corresponding region, but its position varies to some degree.

Remarks—The question of species identity of *Gyraulus laevis* and *G. parvus* has repeatedly been raised because of their conchological similarities. Anatomical investigations show that common shell characters are evidently not a result of convergent evolution, as they share a number of derived characters to the extent that they can be considered sibling species, one living in Europe, the other in North America. The common characters, most of which I regard as derived, are: (1) whorls almost circular in cross section; (2) lack of spiral striation; (3) deeply umbilicated upper side; (4) lack of mantle pigmentation left and right of kidney; (5) black pigmentation of heart, stomach and intestine; (6) lack of marked thickening of penis tip; (7) delicate, irregularly shaped and loosely arranged prostate diverticula; (8) narrow and long bursa copulatrix, and (9) undulate kidney margins.

Of these, characters 7 and 9 are unique in the *Planorbis*-tribe; they have not been observed in related genera, *Anisus, Bathyomphalus,* and *Planorbis*. Placement in their own subgenus is justified. A subgenus name created by Dall (1905: 86) with *Planorbis parvus* Say as the type-species is available: *Torquis.* A diagnosis will be given in a later chapter. According to Dall there are some more species in North America to be placed here. I have not examined other North American species. In Europe, *Gyraulus laevis* is the only representative of *Torquis. G. parvus* is distributed all over North America; "its northern limit corresponds fairly well with the tree line" (Clarke, 1973: 403). As shown here, its range includes Iceland as well. The occurrence in Europe is without doubt due to a quite recent introduction, probably together with aquarium plants. Characters separating *G. parvus* from *G. laevis* are: (1) the elevated penultimate whorl, and (2) the marked widening of the distal half of the vas deferens as compared with that of the proximal half. These two traits of *G. parvus* are unique in the tribus and thus they must be regarded as derived. In addition, (3) the distal portion of the spermoviduct is not wider than the widest portion of the sperm duct, and (4) the euryoekous character of *G. parvus* clearly distinguishes it from *G. laevis.*

My observation that all individuals examined lack an intestinal loop agrees with Baker's (1945: 74) statement "no intestinal loop in *Torquis.*" This may hold true for American species of the subgenus, but not for *Gyraulus laevis.*

Gyraulus rossmaessleri (Auerswald, 1851)

Planorbis rossmaessleri Auerswald, 1851: 179 (Leipzig).

Material—Beside the material dealt with previously (Meier-Brook, 1964), further specimens were studied from Drusenheim (France), 3 specs. (unrelaxed); Sessenheim/Soufflenheim (France), 1 spec.; and Pleistinger Wörth (Germany), 7 specs. (unrelaxed).

Shell—The shell (Fig. 53) is small- to medium-sized, usually not exceeding 4 mm in diameter and 1.3 mm in height. It is similar to *Gyraulus laevis* in shape, but less deeply umbilicate; the sutures are less deep, the whorls are rounded, never angled or keeled. The aperture has a characteristic thickened lip (that does not necessarily terminate growth!). Growth marks indicating growth interruptions are regularly present (desiccation of habitat!). The surface is not smooth, but rather dull, with a very fine reticulate sculpture (spiral striae very close to each other). The color is red-brown.

Animal—The animal is similar to *Gyraulus albus* insofar as diffuse pigmentation is concerned. The heart is not dark, but so sparsely pigmented that it contrasts with its grey surroundings by its light appearance. The kidney has undulate margins. The intestinal loop is present in all individuals. The seminal vesicle is voluminous, with spiny coiling. The distal spermoviduct is long and very slender (Fig. 54). The bursa copulatrix is elongate club-shaped or tapering, in one population (Pleistinger Wörth) being almost of the elongate tadpole type. The bursa duct is wide, not narrower than the vagina. The sperm duct is
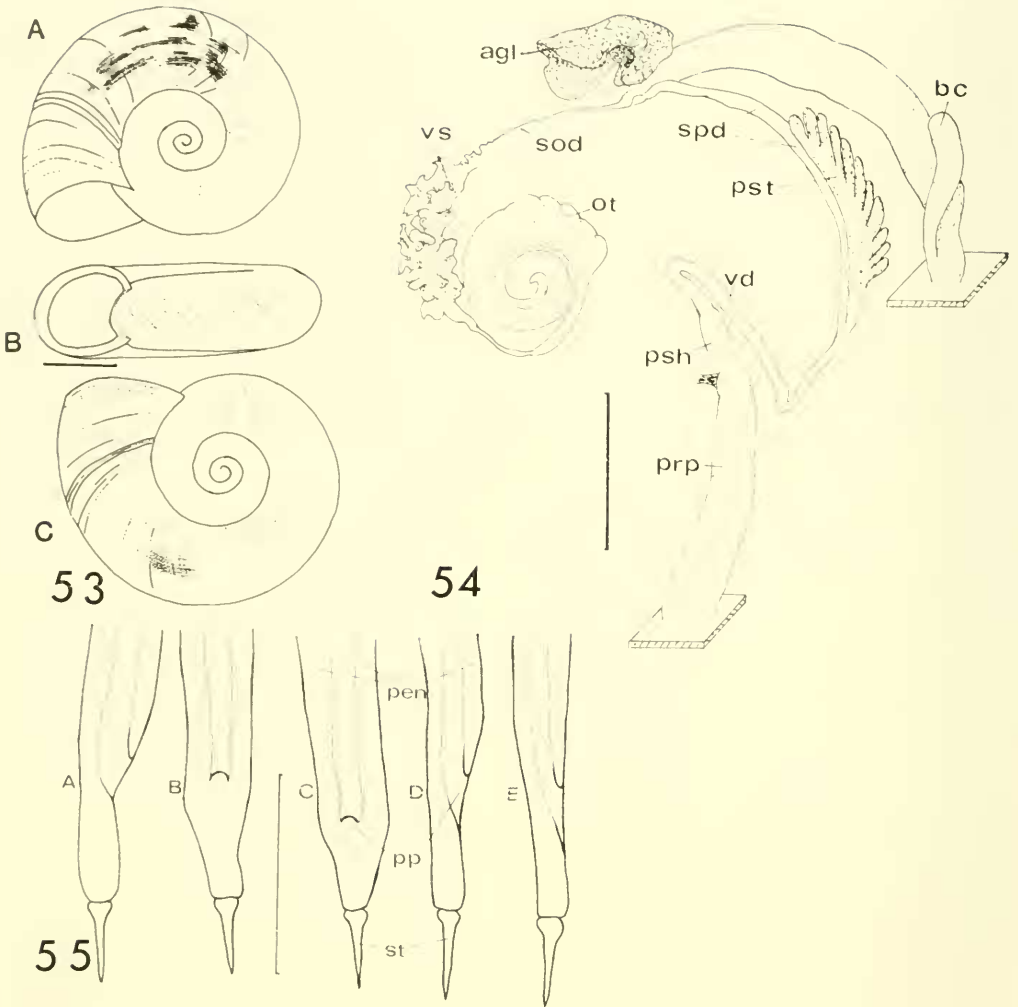
FIGS. 53–55. *G. rossmaessleri.* 53. Shell, Drusenheim. 54. Reproductive system. Soufflenheim. Maximum shell diameter 4.3 mm, 3¾ whorls (M 291). 55. Variation in shape of penis tip and position of penis pore. A: Soufflenheim (M 292); B–D: Pleistinger Wörth (M 293); E: Drusenheim (SMF 246 312). Scale = 0.1 mm.

wide. The prostate gland has a low to moderate number of diverticula (Table 2), which are closely spaced and regular in form. The length of the ♂ copulatory organ is about the same as in *G. albus* or longer (Pleistinger Wörth). The penis sheath which is extremely short and narrow is scarcely set off from the vas deferens. The preputium is considerably wider and longer, the ratio psh:prp being far below one. The penis is correspondingly tiny and slender. The penis tip is tapering where in *G. albus* and other species the thickening

occurs. The penis pore lies where tapering begins. The stylet is hob-nail shaped (Fig. 55).

Remarks—Beside my previous studies on *Gyraulus rossmaessleri* there is only one further paper figuring the reproductive system of this species, as found in a Czechoslovakian population by Hudec (in Macha, 1963: 87). In the shape of the bursa copulatrix, its wide duct, and in the ♂ copulatory organ there is agreement with the present finding. As the status of *G. rossmaessleri* as a separate species had not been acknowledged for a
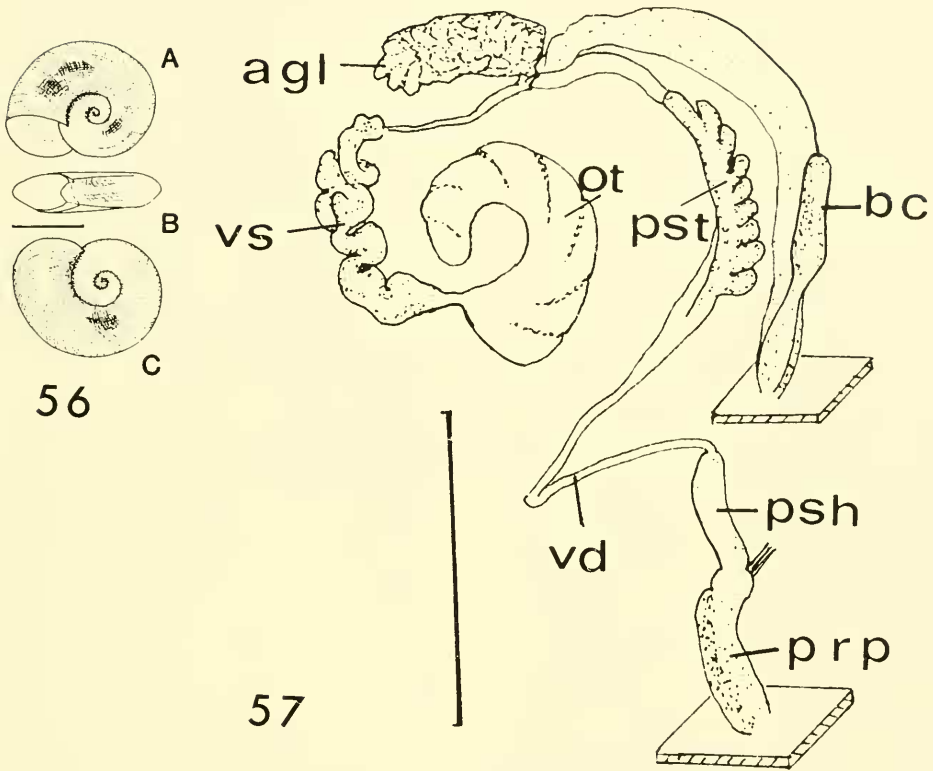
FIGS. 56–57.   *G. riparius,* Kolksee. 56. Shell. 57. Reproductive system. Maximum shell diameter 2.2 mm, 2¾ whorls (SMF 246 313).

long time (compare Meier-Brook, 1964: 233, 238 and following), distribution data in the literature will have to be revised. This is a strictly European species.

Gyraulus riparius (Westerlund, 1865)

Planorbis riparius Westerlund, 1865: 106 (Ronneby).

Material—Kolksee (Germany), 4 specs.

Shell—The shell (Fig. 56) is very small and delicate; most do not exceed 2.3 mm in diameter and 0.6 mm in height; it is discus-like, resembling a young *Hippeutis complanatus* in general shape. The three whorls increase rapidly; they are flattened. The periphery is angled; the aperture is spindle-shaped in its exterior portion. The growth lines are arcuate. The surface is silky in texture and has very fine, but relatively remote spiral striae.

Animal—The animal is weakly pigmented; the cephalopedal mass is light grey, and the mantle including the kidney is almost unpig-

mented. The kidney margins are undulate. An intestinal loop was present in the specimens examined. The ovotestis is large as compared with the remaining parts of the reproductive system (Fig. 57). The proximal portion of the spermoviduct is extremely short. The seminal vesicle has bulbous coils and is very voluminous, approaching or exceeding the albumen gland in size. The bursa copulatrix is elongate club-shaped to cylindrical, its duct being proximally narrow, but inflated towards its orifice, giving it the same width as the vagina itself. The prostate has 7 to 10 diverticula, which are closely spaced and of regular shape. The δ copulatory organ is comparatively long (0.7, 0.8, 0.8, 0.9 mm). The preputium is wide; its lumen is S-shaped. The penis (Fig. 58) is very similar to that described for *Gyraulus rossmaessleri,* with almost no variation in the four individuals.

Remarks—This rare species was placed in *Hippeutis* for a long time. Odhner (1929) was the first to find a stylet and therefore included
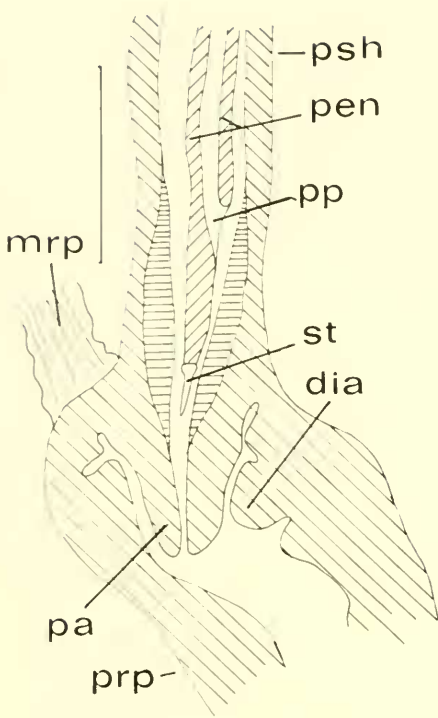
FIG. 58. *G. riparius,* Kolksee, region of transition between penis sheath/preputium and penis tip. Same specimen as in Fig. 57. Horizontal shading: columnar epithelium in distal area of penis sheath. Scale = 0.1 mm. Key to lettering p. 27.

the species in *Gyraulus.* His figure (Odhner, 1929, reproduced in 1956: fig. 2d) shows the general shape of the ♂ copulatory organ found in the German specimens, but (certainly due to the restricted optical facilities then available) his drawing is too poor to permit further comparison in detail.

Because of the ♂ copulatory organ, which undoubtedly was derived from the type seen in *Gyraulus* by size reduction of the penis and penis sheath, and retention of preputium size, it appears justified to place *Gyraulus riparius* in its own subgenus.

Starobogatov (1967: 296) named a new subgenus of *Choanomphalus* (!) with *Planorbis riparius* as the type-species: *Lamorbis.* He also wanted to place *Gyraulus rossmaessleri* in *Lamorbis* but gave no reasons. This will be discussed later.

Gyraulus crista (Linnaeus, 1758)

Nautilus crista Linnaeus, 1758: 709, no. 234.

Turbo nautileus Linnaeus, 1767: 1241, no. 654.
Planorbis imbricatus Müller, 1774: 165, no. 351.
Planorbis paladilhi Moitessier, 1867: 424, pl. 22, figs. 7–14.
Armiger crista, Ehrmann, 1933: 172, fig. 105.
Gyraulus (Armiger) crista, Soos, 1935: 28, fig. 4.
Armiger crista, Baker, 1945: 75, pl. 18, figs. 6–11.

Material—Kuehren (Germany), 15 specs.; Tübingen (Germany), 5 specs.; Wollmatingen (Germany), 4 specs.

Shell (Fig. 59)—The shell is very small, 2.2 to 2.8 (rarely >3 mm) in diameter and 0.75 to 0.9 mm in height. It has 2½ to 2⅞ rapidly increasing whorls. The under side of the whorls are ± flattened; the upper side is well rounded. The periphery is angled, the angle being nearer to the under side. The last whorl does not embrace the penultimate whorl as in all other planispiral species of the genus, but is loosely attached to its upper side, the peristome thus being continuous. The shell is almost flat or very slightly convex on its under side and deeply concave on its upper side. The whorls are traversed by ridges, these sometimes carrying periostracal fringes projecting peripherally (Fig. 59B). Reticulate sculpture is absent.

Animal—The animal is weakly pigmented, the cephalopedal mass being light grey and the mantle showing a light and diffuse pigmentation. The kidney margins are distinctly undulate. An intestinal loop was present in all specimens studied. The ovotestis and seminal vesicle vary in size. The female tract is short and wide (Fig. 60). The bursa copulatrix is long and slender and is club-shaped. The prostate diverticula are reduced in length, so that the gland merely consists of the prostate duct (Fig. 60B); only in one of the individuals studied were there vestiges of 7 diverticula (Fig. 60A) that indicated that, before reduction, these must have been regularly and densely arranged. The penis sheath is long and slender, being always longer than the preputium (compare Table 2). The diaphragm is very muscular, giving the knoblike thickening between the penis sheath and the preputium a particularly pronounced look. The penis has a conical tip and a hob-nail stylet (Fig. 60C, D). The penis pore lies near the tip.

Remarks—The reproductive system of this well-defined species was previously figured
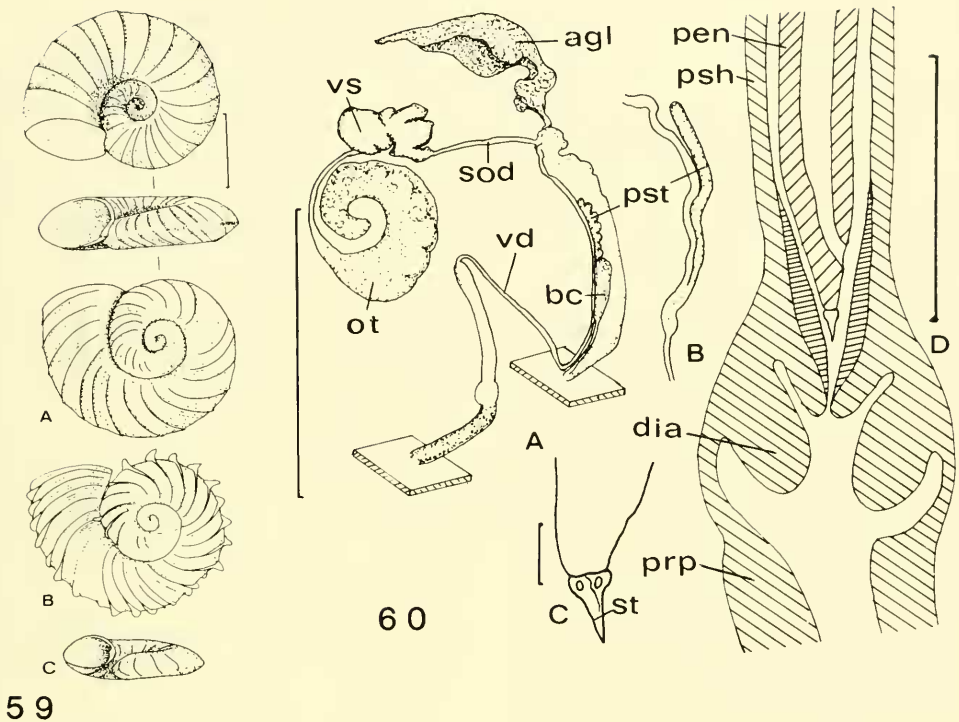
FIGS. 59–60.   G. crista. 59. Shell. A—ditch near Wallnau/Fehmarn (SMF 248 548); B—form found in lenitic biotopes, Wollmatingen (SMF 248 547); C—lake form, Dobersdorfer See (SMF 248 549). 60. A—reproductive system, Kuehren (SMF 248 543); B—prostate gland of another specimen from Kuehren (SMF 248 543); C—penis tip with stylet, Tübingen (M 302); D—middle part of ♂ copulatory organ, Kuehren, shading as in Fig. 58 (M 313). Scales: 1 mm in A and B, 0.01 mm in C, 0.1 mm in D.

by Soos (1935: fig. 4) and Baker (1945, pl. 18). There is general agreement with the present findings. Differences concerning the armament of the penis tip and the form of the prostate gland exist between Baker's (1945) figures and my findings. Soos showed 9 and Baker 13 prostate diverticula of normal length. There is possibly greater variation in this character than seen in the material I studied, but considering the smallness of the animal, I consider the possibility that the presence of well-defined and long prostate diverticula in all closely related taxa fired these authors' imagination. This is more plausible considering that in contracted animals transverse folds are commonly found in the female tract to which the prostate gland adheres. Greater concentrations of pigment cells at these sites could indeed simulate the picture of prostate diverticula.

Gyraulus crista has usually been regarded as a member of a separate genus, Armiger. This idea was based on the really aberrant form of the shell and supported by the statements of previous students who did not recognize a penial stylet. Baker (1945: 76) spoke of a "pointed fleshy papilla" instead of a stylet, and Odhner (1956) observed what he called a "small cuticular cap" or a "bulbous tip." The alleged lack of a stylet led both authors to exclude the species from Gyraulus. The only publication mentioning the presence of a stylet in G. crista was the one by Hubendick (1955: 466), but Odhner (1956) believed that Hubendick had mistaken a G. riparius for G. crista, arguing that Armiger crista did not occur in Hubendick's collecting place. Whatever may be the truth, the smallness of the two species in question may have hampered thorough studies. In light section the true nature of the stylet must indeed remain obscure. Only an extraction of the penis from

FIG. 61.   *G. acronicus.* Bodensee near Überlingen (loc. typ.), shell.

its sheath, which was successful for the first time during the present studies, revealed that the armament of the penis tip in *G. crista* does not differ fundamentally from that in *G. riparius* and *G. rossmaessleri.* In one stylet of *G. crista* (Fig. 60C) there is even a tinge of the brown colour typical for the stylet of *Gyraulus.* Other features, found with the aid of oil immersion and phase contrast microscopy, are the well-defined border between the penis tissue and the base of the stylet, two double refractive areas in the base and a trace of a longitudinal line indicating that the stylet is formed by a rolled blade as in those other taxa of the *Planorbis* tribe which are equipped with a stylet. Therefore, there is no doubt that

the stylet of *G. crista* has the same origin as the stylet in any other *Gyraulus* species.

The possession of such a stylet alone would not necessarily place the species in the genus *Gyraulus,* as I shall explain later. But, besides the shell character state "rapidly increasing whorls" there is at least one other feature that leaves no alternative but placing *Nautilus crista* in *Gyraulus,* i.e. the distinctly undulate kidney margin. As will become clearer in the cladistic analysis, the undulate kidney margin is a character very probably having evolved only once in the *Planorbis* tribe. It does not occur in any others of its genera. *G. crista* must have evolved from a parent species carrying this character state. This stem species must have been identical or a descendant of the one from which the species *G. parvus, G. laevis, G. rossmaessleri,* and *G. riparius* evolved. According to Hennig's quite correct and convincing arguments against Mayr's (1974b) criticism (Hennig, 1974), a taxon can only be regarded as monophyletic if *all* descendants of one parent species are included in this taxon. Accordingly *G. crista* must not be grouped in a separate genus.
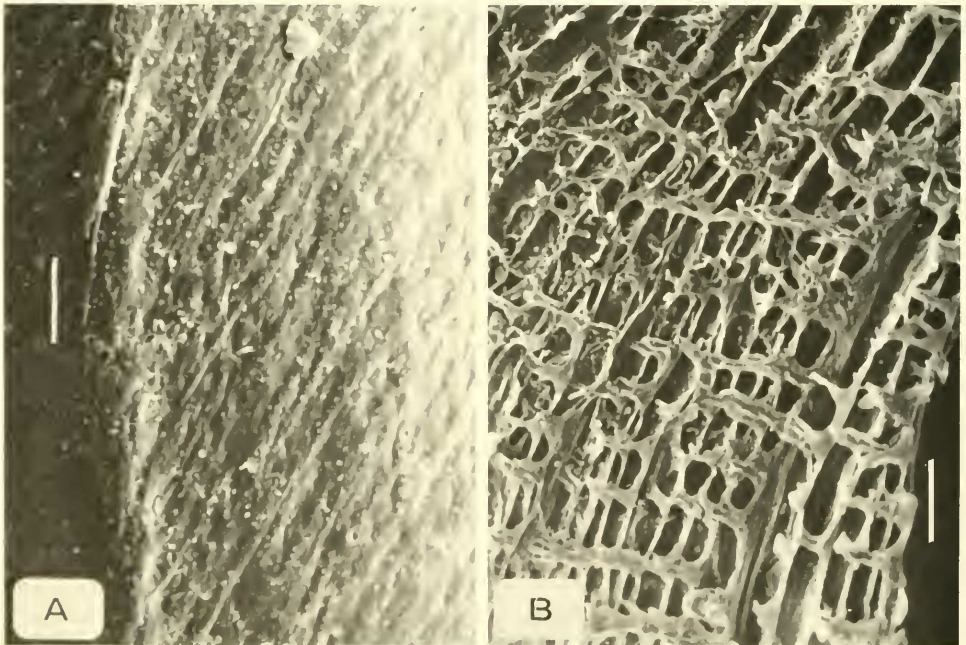
FIG. 62.   *G. acronicus,* shell surface. A—Bodensee, faint spiral striae and weak keel; B—Vikarsjön, "hairs" protruding from periostracal ridges on growth lines. Scale = 0.1 mm.
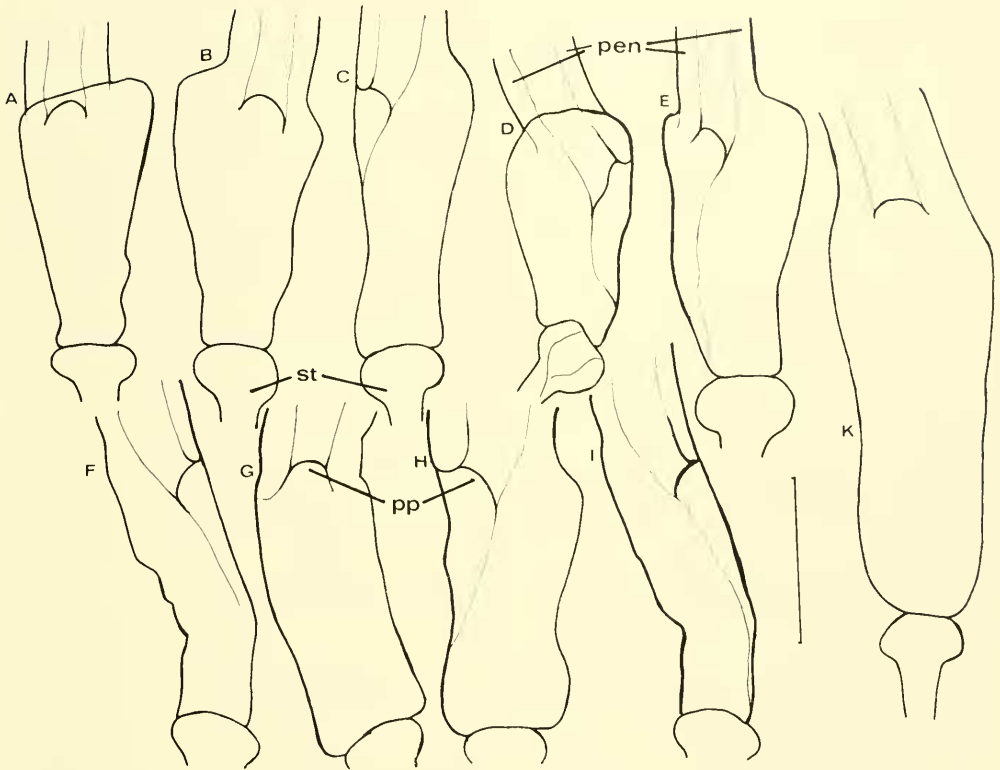
FIG. 63. *G. acronicus*, variation in shape of penis tip and position of penis pore. A—Tärna; B—Ragunda; C—Tulom; D—Krasnojarsk; E—Valtjärn; F—Ragunda; (A–F unrelaxed; microscopic preparations under respective reg. no. in museum collections, see Appendix); G—Siggen (M 46); H—Dobersdorfer See (M 41); I—Vikarsjön (unrel.); K—Bodensee (M 48). Scale = 0.1 mm.

Gyraulus acronicus (Férussac, 1807)

Planorbis acronicus Férussac, 1807: 105 (Bodensee near Überlingen).
Gyraulus deformis Hartmann, 1844: 95, pl. 27, figs. 1–5.
Planorbis gredleri Gredler, 1859: pl. 5, figs. 1a–d.
Planorbis borealis (Lovén Ms) Westerlund, 1875: 77–79.
Gyraulus albus acronicus, Ehrmann, 1933: 170, pl. 7, figs. 107, 107a.
Gyraulus gredleri, Ehrmann, 1933: 171, pl. 8, figs. 106, 106a.
Gyraulus albus deformis, Jaeckel, 1962: 68.
Gyraulus acronicus, Jaeckel, 1962: 69.

Material—In addition to the material previously studied (Meier-Brook, 1964: 235), unrelaxed snails were available from the following localities, partially under the name

Planorbis borealis Lovén: Sweden: Vikarsjön, 2 specs.; Ragunda, 3 specs.; Valtjärn, 2 specs.; Vojmån, 3 specs.; Tärna, 3 specs.; USSR: Karabella, 2 specs. (named *Gyraulus rossmaessleri,* det. Westerlund); Tulom, 3 specs. (named *borealis,* det. Odhner); Dudinska, 1 + 2 specs. (2 lots; named *borealis,* det. Odhner); Krasnojarsk, 3 specs. (named *borealis,* det. Odhner); Paratunka, 2 specs. (unnamed).

Shell—The shell (Fig. 61) is large, usually reaching 7 mm in diameter or more and 2 mm in height; it has 4–4¾ whorls, is not deeply umbilicate, with sutures not deep and whorls flattened. The periphery is angled or rounded, sometimes with a small periostracal fringe. The aperture is ellipsoid, usually oblique. The last whorl is regularly deflected, thus giving the shell the appearance of being deformed. The surface is dull, and is reticulately sculp-
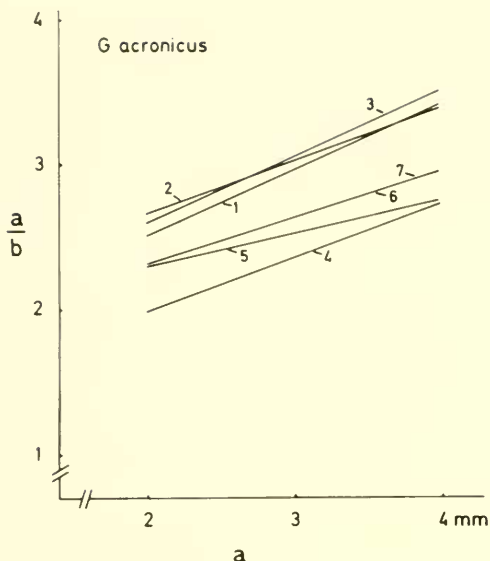
FIG. 64. *G. acronicus,* a/b plotted against a in three central European and four N European or N Asiatic populations. 1—Bodensee (n = 117); 2—Siggen (n = 38); 3—Dobersdorfer See (n = 40); 4—Vojmån (n = 25); 5—Tulom (n = 13); 6—Rasno-volok (n = 14); 7—Krasnojarsk (n = 18). Correlations significant: no. 5: $p < 0.05$, all other samples: $p < 0.001$.

tured. The sculpture sometimes is almost indiscernible, sometimes stronger, but never coarse as in *Gyraulus albus*. Spiral striae are less remote than in *G. albus*. Fine periostracal "hairs" can be present (Fig. 62). The color is light-corneous, like *G. albus*.

Animal—The animal is moderately grey on the cephalopedal mass. The mantle roof has a distinct pattern, which is sometimes weakly developed. The kidney margins are straight. An intestinal loop was developed in all individuals checked. The seminal vesicle varies in shape. The bursa copulatrix is elongate club-shaped. The prostate gland has a high number of diverticula (compare Table 2), which are closely spaced, have a regular shape and are unbranched. The ♂ copulatory organ is very long (Table 2) and usually bent twice (Meier-Brook, 1964: figs. 6–10) The penis tip can be faintly thickened. The penis pore lies near the proximal end of the thickening or in its proximal half (Fig. 63).

Remarks—*Gyraulus acronicus* was long considered a peculiar lake form of *G. albus*

until its identity with *G. gredleri* was proved by Odhner and Forcart (compare Meier-Brook, 1964). *G. borealis* (Lovén, Ms) (Westerlund, 1875) was for a long time recognized as a larger boreal-subarctic form of *G. gredleri,* and now of *G. acronicus.* It cannot be overlooked that *G. borealis* is persistently different in shell characters from the temperate European forms of *G. acronicus.* In central Europe the whorls of *G. acronicus* are flattened, the last whorl is more deflected, the periphery is distinctly angled or weakly keeled. In N Europe and boreal-subarctic Asia, the whorls are more rounded, the last whorl is less deflected, the periphery slightly angled though often decorated by a delicate periostracal fringe.

A latitudinal cline is demonstrated in Fig. 64, where flatness and relative height increase are expressed by regression lines for 3 central European (1–3) and 4 boreal-subarctic samples.

Gyraulus acronicus is the largest European species of the genus. It is characterized by the long, slender and bent ♂ copulatory organ and by its mantle pigmentation, showing a distinct pattern although this is less strong than in *G. chinensis* (Fig. 12). It is the only European indigenous species with such a pattern. Hubendick's (1955: 479) misidentification of *G. albus* as *G. acronicus* was pointed out previously (Meier-Brook, 1964: 236). The only study of the anatomy of this species from outside central Europe is the one published by Khazannikov (1973, fig. 4) from River Erek Basin, Caucasus. In the shape of the figured ♂ copulatory organs there is close agreement with my previous figures of *G. acronicus* (Meier-Brook, 1964, figs. 6–10). Khazannikov's printed drawings, however, are too poor to allow comparison of internal details.

Final Notes on European Species

The main results of anatomical studies on the European *Gyraulus* species, except the endemic species from Macedonia, which will be dealt with in a separate chapter on ancient lakes species, are summarized in Table 2. Provisional grouping into subgenera will be substantiated after discussion of relationships between all taxa studied (see below). A key is included as an aid to identification of species indigenous to or introduced to Europe outside the Macedonian lake basin. It is based on diagnostic characters. These are

not necessarily indicators of relationship. The dendrograms (Figs. 107, 111, 112) showing phylogenetic relationships are suitable for identification as well.

Key to the *Gyraulus* Species Living in Europe Excluding Macedonia

1A. Periphery angled 2
1B. Periphery rounded 5
2A. Shell diameter not exceeding 3 mm; mantle pigmentation diffuse or lacking; kidney with undulate margins 3
2B. Shell diameter exceeding 4 mm, mantle pigmentation with distinct pattern, kidney margins straight 4
3A. Angle approximately in the middle between upper and under side; shell therefore discus-shaped; surface with silky lustre; penis sheath shorter than preputium, not widened proximally; prostate gland with 7 to 10 regular diverticula which are densely arranged . . . . *G. (L.) riparius*
3B. Angle near under side, therefore shell ± flat on under side, whorls well rounded on upper side; last whorl not embracing the penultimate, but loosely attached to its upper side; whorls traversed by ridges (costae) at greater intervals; sometimes ridges peripherally projecting to spiny lamellae; penis sheath longer than preputium; prostate diverticula lacking or vestigial . . . . *G. (A.) crista*
4A. Shell rough and not glossy, usually with distinct reticulate sculpture, spiral striae relatively distant; prostate gland with 20 to 40 diverticula; pigmentation of mantle poor in contrast . . . . *G. (G.) acronicus*
4B. Shell smooth and glossy, at most faintly reticulate sculpture, then spiral striae very fine and dense; prostate gland with 8 to 20 (exceptionally up to 24; in Europe so far only between 12 and 18) diverticula; pigmentation pattern on mantle distinct and rich in contrast; introduced from Asia to rice fields in N Italy and Camargue; also found in West Frisia (Netherlands) . . . . *G. (G.) chinensis*
5A. Shell surface smooth, glossy, aperture rounded, kidney margins undulate, ♂ copulatory organ 1 to 2 mm long, penis sheath distinctly longer than preputium, widening proximally, prostate diverticula mostly irregular and not closely spaced 6
5B. Shell surface with fine or coarse spiral striation or, if appearing glossy, aperture with white lip; kidney margins straight or undulate; ♂ copulatory organ of varying length; penis sheath distinctly shorter and narrower than preputium, not widening proximally, prostate diverticula regular and closely spaced 7
6A. Penultimate whorl distinctly elevated, distal portion of spermoviduct slender, not wider than widest portion of sperm duct; distal half of vas deferens much wider (2:1 on an average) than proximal half (introduced from N America) . . . . *G. parvus*
6B. Penultimate whorl not or not distinctly elevated, distal portion of spermoviduct wider than widest portion of sperm duct and vas deferens, distal half of vas deferens not conspicuously widened (1:1) . . . . *G. laevis*
7A. Aperture circular, with white callous lip, shell surface with very fine spiral striation, almost glossy, color red-brown, penis sheath distinctly shorter and narrower than preputium, not widening proximally, penis narrowing distally . . . . *G. rossmaessleri*
7B. Aperture ovoid, without callous lip, shell surface with fine or rough spiral striation, color whitish to light-corneous, penis sheath distinctly longer than preputium, widening proximally, penis thickening distally 8
8A. Shell with fine spiral striation, prostate gland with 20 to 40 diverticula, ♂ copulatory organ longer than 2 mm, usually bent twice (S-form), penis pore near proximal end of thickened penis tip or in its proximal half . . . . non-angled form of *G. acronicus*
8B. Shell with coarse spiral striation, prostate gland with less than 22 diverticula, ♂ copulatory organ shorter than 2 mm, bent at most once, penis pore subterminal in thickened penis tip or in its distal half . . . . *G. albus*
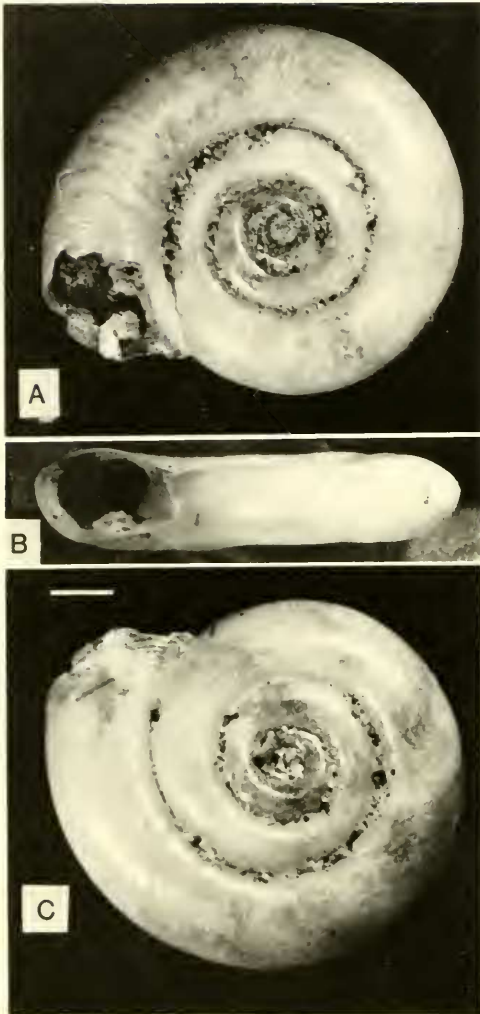
FIG. 65.   *G. euphraticus,* Samava, lectotype ZMZ
521 181.

SPECIES OF SOUTH AND
EAST ASIA

Before conclusions are drawn as to species
delimitations material is treated under prelim-
inary names that are widely used in the liter-
ature.

Gyraulus euphraticus (Mousson, 1874)

Planorbis (Gyraulus) devians Porro var. *eu-
phratica* Mousson, 1874: 40 (Samava/Eu-
phrates).

The original series on which Mousson's
description is undoubtedly based (Mousson's
handwriting kindly confirmed by Dr. Zilch)
consists of two lots with identical labels. One
contains hundreds of shells, obviously un-
sorted (ZMZ 521 180) and mixed with mud
particles, in the other one (ZMZ 521 181)
Mousson has sorted out 33 specimens
(probably the "beautiful" ones, as usual at
that time). A lectotype has been selected from
the latter one (Fig. 65). A second specimen
from lot no. 521 180 is also figured here (Fig.
66) to demonstrate the extreme conchologi-
cal variation in the original series. There are
all transitional shell forms between the fig-
ured ones, and the full range of variation is
even wider. No gap is visible within the range.

Material—S Iran, 30 specs.

Dr. Massoud, who kindly put at my dispos-
al living snails and preserved specimens from
the collecting site in S Iran was unable to give
more precise information on the locality. The
stock had been kept in his laboratory for par-
asitological research since previous epidemi-
ological surveys in Khuzistan. At least this is
not far distant from the type-locality of *Gy-
raulus euphraticus.* The shell form in this
stock resembles Mousson's original series
and can therefore be identified with his
species (Fig. 85, lines 7 + 8). The following
description is based on both series, as far as
shell characters are concerned.

Shell—The shell is of medium size, the
maximum diameter scarcely reaching 7 mm;
it is rather flat (<1.5 mm high). As the last
whorl is only exceptionally deflected, it is
possible to give a reliable figure of the ratio
maximum diameter : height: in 100 randomly
selected shells between 2.5 and 5.2 mm di-
ameter and mean values of 3.76 and 1.10
mm (ZMZ 521 180) it is 3.42. Three and a
half to 4½ whorls are rapidly (Fig. 66) or
slowly (Fig. 65) increasing, in the latter case
nearly approaching *Anisus* in appearance.
The whorls are slightly or considerably wider
than high. The periphery is angled. The shell
is not deeply umbilicate. The surface is
smooth, glossy; no reticulate sculpture is
present. The color is light-corneous.

Animal—The animal is light grey, the man-
tle pigmentation showing a distinct pattern,
similar to that figured in *Gyraulus chinensis*
(Fig. 12). The kidney margins are straight. An
intestinal loop is absent or reduced in size.
The seminal vesicle is bulbous (Fig. 67) or
slightly spinous. The bursa copulatrix has a
spherical club shape and is sometimes taper-
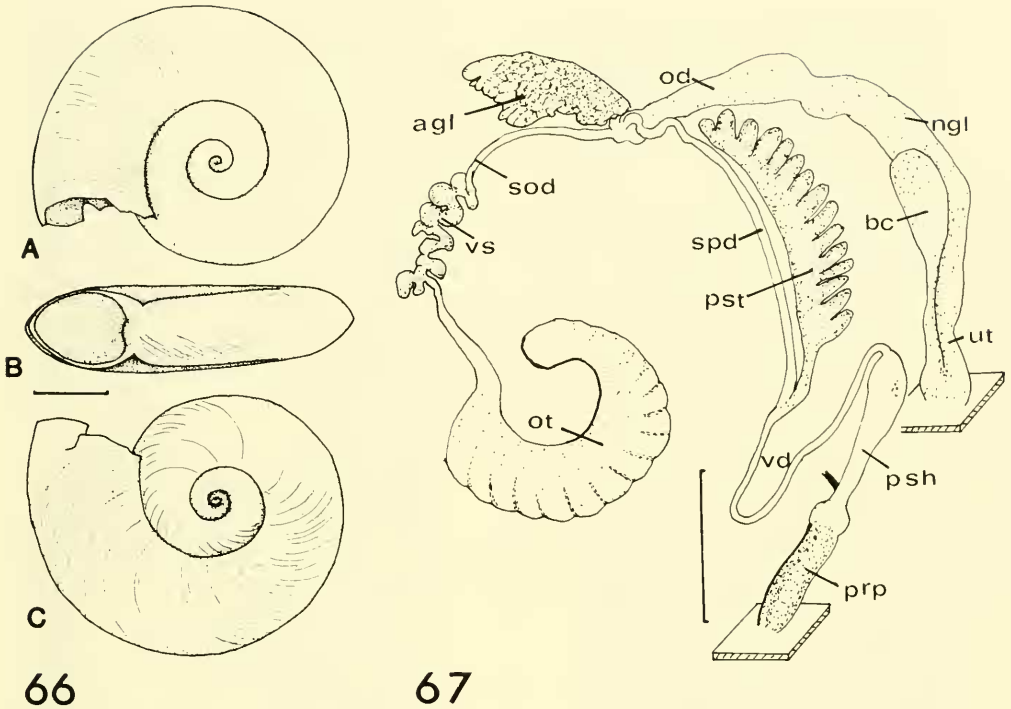
FIGS. 66–67. *G. euphraticus*. 66. Samava, paralectotype (ex ZMZ 521 180). 67. S Iran. Reproductive system. Maximum shell diameter 3.7 mm, 3½ whorls (M 121).

ing though inflated at its upper end. The vagina is inflated in most specimens. The prostate gland bears 9 to 18 diverticula (cf. Table 6). The ♂ copulatory organ is similar to that of *G. acronicus* in general, but shorter, bent no more than once with the penis sheath relatively longer (cf. Tables 2 and 6). The penis tip and the position of the penis pore are indistinguishable from those in *G. acronicus*. Preputial pilasters are present.

Remarks—Mousson's description is so insufficient ("Fere regularis, pallide corneo-hyalina"), like most attempts at verbal characterizations of shells, and moreover, the description suggests similarity to *Gyraulus devians* Porro (which is probably a synonym of *G. acronicus*) that misidentifications are understandable. The first and as yet only anatomical account of a snail called *G. euphraticus* was published in 1919 by Annandale & Prashad. These authors, complaining about frequent confusions, "because conchologists have rarely seen specimens from the original localities" (Annandale & Prashad, 1919: 52) probably succumbed to the same error. The

shell figured from Quetta, Baluchistan, (30°15′N; 67°00′E), and said to "agree closely with shells of Mousson's *G. devians* var. *euphratica* recently collected by Captain C. L. Boulenger in Mesopotamia," measures 8.9 mm in max. diameter and 2.55 mm in height(!). It does not fall in the range of variation shown in Mousson's original series. Moreover, the distance between Quetta and Samava is 2160 km, and there are large deserts between the localities, so that great doubts arise as to their identification. The figures of the reproductive system prove that the animals dissected were indeed *Gyraulus* but further details are lacking due to the insufficient optical facilities of that time. The fact, by the way, that Annandale & Prashad's fig. 5D—of a penis sheath of *G. euphraticus* (according to the caption)—is not that of a *Gyraulus,* is evidently due to an accidental exchange of letters D and F. The shell figured by Annandale & Prashad (1919: fig. 7A) is so similar in size, shape and proportions to shells in the British Museum of Natural History (no registration number) under the name of *Plan-*

TABLE 6. Reproductive organs of *Gyraulus* in S and E Asia.

Provis. species name, locality	No. prost. diverticula			Male copulatory organ				
				Total length (mm)			Ratio psh:prp	
	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.
euphraticus, S Iran	16	9–18	13.1 ± 2.5	18	1.6–2.6	2.1 ± 0.2	1.3–2.9	1.9 ± 0.5
hebraicus, Kumluca + Limyra[1]	6	11–15	13.3 ± 1.4	10	1.2–1.9	1.6 ± 0.2	0.8–2.3	1.4 ± 0.4
piscinarum, Diyarbakir[1]	4	12–16	14.0	4	1.8–2.7	2.4	1.2–2.0	1.5
mareoticus, Cairo	18	14–19	16.6 ± 1.4	13	1.9–2.8	2.5 ± 0.3	1.4–2.3	1.9 ± 0.3
Alexandria[1]	4	15–19	17.3	4	1.2–2.0	1.8	1.2–2.2	1.6
convexiusculus, Maur. + Afgh.[1]	7	12–15	13.8 ± 1.1	8	1.2–2.1	1.7 ± 0.4	1.3–1.6	1.4 ± 0.2
India[1]	4	20–24	22.3	6	1.5–2.7	1.9	1.0–1.3	1.2
Thailand[1]	5	10–15	12.7 ± 2.5	7	1.1–1.6	1.35 ± 0.3	1.3–1.8	1.6 ± 0.1
chinensis, Hong Kong[1]	8	11–15	12.9 ± 1.7	13	1.1–2.3	1.45 ± 0.3	1.1–2.1	1.5 ± 0.4
spirillus, Onna-son[1]	5	12–16	14.0 ± 1.6	5	1.4–2.0	1.7 ± 0.3	1.1–1.7	1.4 ± 0.3
Motobu-cho[1]	5	16–20	17.8 ± 1.6	5	1.7–2.6	2.0 ± 0.4	1.2–3.2	2.0 ± 0.7
Taiwan	54	11–21	15.7 ± 2.1	33[2]	1.4–3.0	2.0 ± 0.3	1.1–2.6	1.6 ± 0.4
Chongpyong	15	8–18	14.0 ± 2.4	15	1.6–2.7	2.1 ± 0.3	1.1–2.0	1.6 ± 0.3
Kaejong	4	13–16	14.0	5	1.4–2.3	2.0 ± 0.4	1.4–2.4	1.9 ± 0.4
Kunsan	8	9–19	14.0 ± 3.0	8	1.9–3.7	2.5 ± 0.6	1.3–2.3	1.6 ± 0.3
tokyoensis, Tomigusuku-son[1]	10	11–18	15.0 ± 2.3	13	1.6–2.7	2.1 ± 0.4	1.1–2.6	1.9 ± 0.5
Sashiki-son[1]	7	12–19	15.6 ± 2.3	7	1.4–2.2	1.9 ± 0.3	0.9–1.8	1.5 ± 0.3

[1] Unrelaxed.
[2] Unrelated individuals excluded.

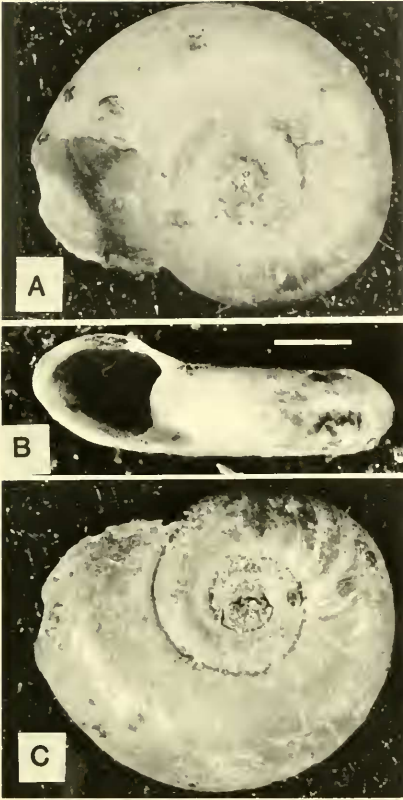FIG. 68. *G. hebraicus,* Bahr el Houlé, Syria; lectotype (MHN Genève).

FIG. 69. *G. piscinarum*, Baalbeck, Lebanon; lectotype (MHN Genève).

orbis nanus that species identity is probable. The lot is labelled: "*Planorbis nanus* Sowerby, Loc. Ganges, India. H. Cuming colln. 3 specs, Acc. no. 1829—Apparently not the specimens figured in Reeve, Conch. Icon. XX, *Planorbis,* Pl. 9, Sp. 75." The largest of the 3 shells measures 8 mm in diam. and 2.5 mm in height. The anatomy of *P. nanus,* however, could not be examined for comparison.

The question of a relationship between *G. euphraticus* and *G. chinensis* will be discussed later.

Gyraulus hebraicus (Bourguignat, 1852)

Planorbis hebraicus Bourguignat, 1852: 23, Nr. 3 (Bahr-el-Houlé, Syria).

A lectotype is designated here from Bourguignat's original lot in Musée d'Histoire Naturelle Genève (no registration number) labelled "*Planorbis hebraicus* Bourg., type, Bahr-el-Houlé (Syrie)" (Bourguignat's handwriting kindly identified by Dr. Zilch). The lot contains 2 shells of 5.9 mm diameter and 1.55 mm height, and 4.85 mm diameter and 1.50 mm height; the smaller one has been selected (Fig. 68).

Material—Since alcohol material from Syria or Lebanon was not obtainable, material tentatively identified as G. *hebraicus* from the geographically least distant localities in Turkey was examined: Kumluca, 2 specs., Limyra, 8 specs. (all unrelaxed).

Shell—The shell (Fig. 68) is small to medium-sized, rather flat, usually 3 to 5 mm in diameter and 1.2 to 1.6 mm in height with 3¼ to 4 whorls which increase rather rapidly, flattened and wider than high. The shell is equally concave on both sides. The periphery is slightly angled. The surface is smooth, glossy; reticulate sculpture is absent. The color is light-corneous.

Animal—The animal is light grey, the mantle pigmentation showing a distinct pattern

that is marbled but not as contrasting as in Fig. 12. The kidney character state was not determined in the contracted animals. An intestinal loop was present in all individuals. The bursa copulatrix has a club shape. The prostate gland bears 11 to 15 closely spaced and regular diverticula. The ♂ copulatory organ, as judged from the contracted material, is not much shorter than in *Gyraulus euphraticus* (Table 6), the ratio penis sheath : preputium similar to that in *G. euphraticus*. The position of the penis pore was not discerned due to poor fixation.

Remarks—There are few records of *Gyraulus hebraicus* in the literature. Beside the type lot there is one other lot in MHNG identified by Bourguignat from "fossés près du camp Deer (almost illegible) pins, près de Beyrouth. Mahmoud," containing 7 shells. The shells are similar to those of *G. euphraticus*, though slightly higher. If the material anatomically examined were from the type-locality I should not hesitate in considering *euphraticus* a junior synonym of *G. hebraicus*. But before a widely used name such as *G. euphraticus* is withdrawn, one should wait for an opportunity to study topotypes of *G. hebraicus*.

Gyraulus piscinarum (Bourguignat, 1852)

Planorbis piscinarum Bourguignat, 1852: 22, no. 2 (Baalbeck, Lebanon).

A lectotype is designated here (Fig. 69) from the lot labelled "type" by Bourguignat (MHNG, no registration number), from Baalbeck. The lot includes 63 paralectotypes.

Material—Diyarbakir (Turkey) 5 specs. (unrelaxed).

Shell—The shell is of medium size, 5 to 6 mm in diameter, and relatively high due to a largely deflected last whorl, with a height often up to 2.5 mm. Three to four whorls rapidly increase. The whorls are not flattened (Fig. 85, regression line 2). The periphery is rounded or at most slightly angled (Fig. 70). The under side is convex and hardly umbilicate. The upper side is deeply umbilicate. The last whorl is slightly to strongly deflected. The aperture is oblique. The surface is moderately smooth and silky. In the sample anatomically examined there is very faint reticulate sculpture. The color is dark-corneous to light brown. *Gyraulus piscinarum* is pronouncedly thick-shelled.

Animal—The animal is dark grey, with diffuse and dark mantle pigmentation. The kid-

ney margins are straight. An intestinal loop was present in the individuals seen. The ovotestis is large (Fig. 71). The seminal vesicle is of the usual size and spinous. The bursa copulatrix is of the spherical tadpole type, with a long and narrow duct. The prostate gland bears 12–16 closely spaced, fleshy diverticula. The vas deferens is equally narrow over its full length. The ♂ copulatory organ is relatively long (Table 6), with a varying ratio penis sheath : preputium. The penis tip has normal thickening, the penis pore being situated in its middle part or the proximal half (Fig. 72).

Remarks—*Gyraulus piscinarum* is a well-defined species, even on purely conchological grounds. Its convex under side makes it one of the most easily recognizable species in the genus. It is the only Asiatic species seen in this study having diffuse mantle pigmentation. Its bursa copulatrix of the tadpole type seems to be a species-specific character state. Nevertheless, *G. piscinarum* has often been confused in the literature and in collections. Bourguignat himself erroneously used this name for material of two lots. One contained one specimen from "fossés près de Beyrouth, Mahmoud" (probably from the same locality as *G. hebraicus*, see above), which is *G. hebraicus*. The other lot from "le Danube à Ibraila" contained one shell of *G. rossmaessleri*. Records of *G. piscinarum* in the literature are quite common, but in my opinion Bourguignat's types were insufficiently known to many authors, and *G. piscinarum* probably has a wider distribution in the literature than in nature.

Gyraulus ehrenbergi (Beck, 1837)

Planorbis ehrenbergi Beck, 1837: 119.
Planorbis mareoticus Innes, 1884: 339.

Material—Cairo (Egypt) 13 specs.; Alexandria (Egypt) 4 specs. (unrelaxed).

Shell (Fig. 73)—The shell is small, usually not exceeding 4 mm in diameter, but relatively high: 1.3 mm (Fig. 85, line 1); 3½ whorls increase rapidly. The periphery is slightly angled, with a small, but distinct fringe of periostracum. The last whorl is scarcely deflected. The surface is smooth and silky. Growth lines are very fine. No reticulate sculpture is present. The color is pale-whitish.

Animal—The animal is almost hyaline, almost lacking pigment. The cephalopedal mass is almost white. The mantle pigmenta-
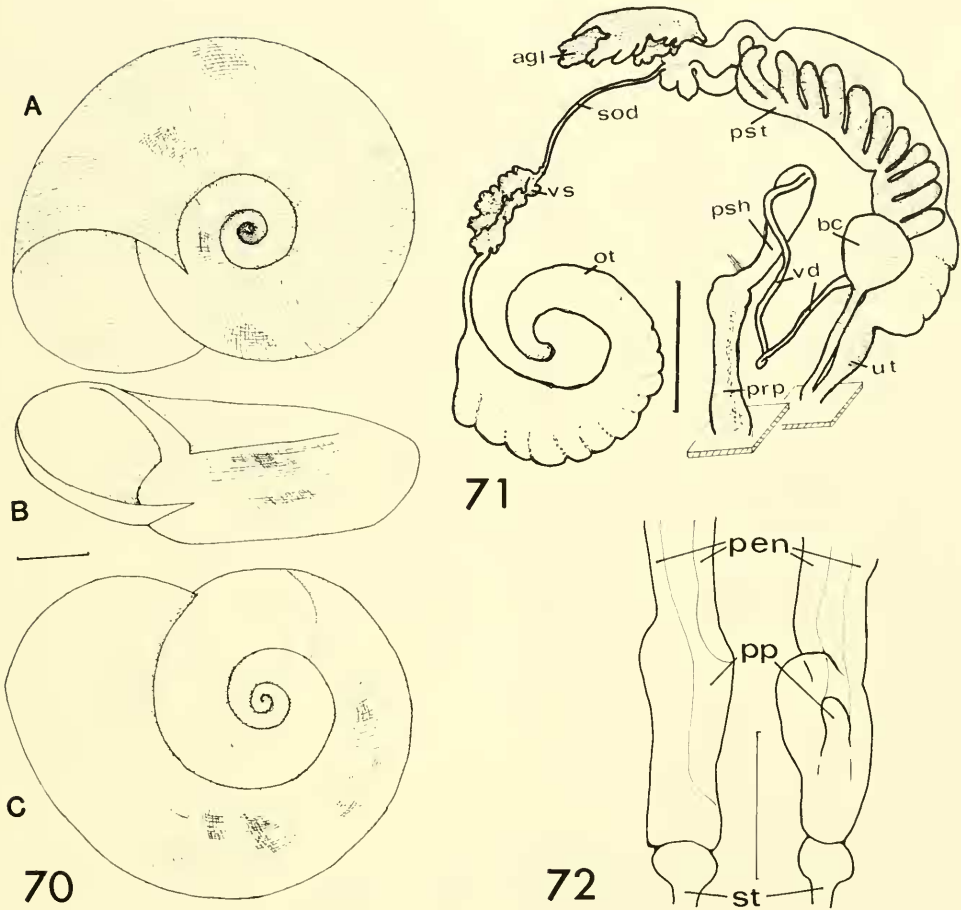
FIGS. 70–72. *G. piscinarum*, Diyarbakir. 70. Shell (SMF 246 318). 71. Reproductive system; maximum shell diameter 5.0 mm, 3⅔ whorls (SMF 246 317). 72. Penis tips (M 294). Scale = 0.1 mm.

tion has a distinct, though weakly developed, pattern. The kidney, heart, stomach and preputium which in most other *Gyraulus* species are darkly pigmented, bearing only scattered black spots. The kidney margins are straight. An intestinal loop is present. The bursa copulatrix is of the elongate club type, with a duct about half as wide as the bursa itself (Fig. 74). The prostate gland bears 14 to 19 diverticula (Table 6), which are closely spaced. The vas deferens is equally narrow over its full length. The ♂ copulatory organ is relatively long. The ratio penis sheath : preputium is high (Table 6). The penis tip is normally thickened, the penis pore lying in its proximal half.

Remarks—The snails studied of the Egyptian populations belong to a well-defined species, without close affinity to the W Asiatic species dealt with on the preceding pages. Apart from their relative height they do not have many character states in common with *Gyraulus piscinarum,* as might be implied by Jaeckel's (1962: 104) considering *G. piscinarum* as a subspecies of *G. ehrenbergi. G. ehrenbergi* differs from G. *piscinarum* not only in shell characters, but also in pigmentation, width of the bursa duct and numbers of prostate diverticula.

A close relationship of *Gyraulus ehrenbergi* with other African species, anatomically known as *G. costulatus* (Krauss) and *G. connollyi* Brown & van Eeden, is improbable. For comparison, *G. costulatus* is briefly characterized below.
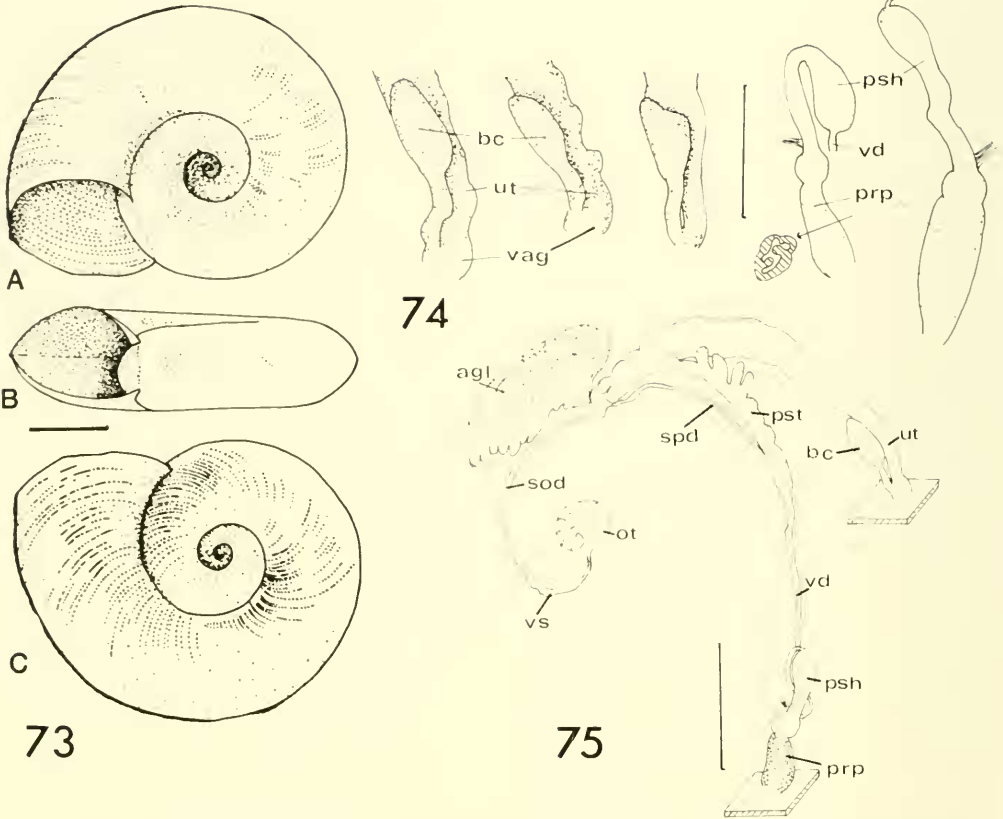
FIGS. 73–75. *G. ehrenbergi*, Cairo, shell (SMF 246 319). 74. *G. ehrenbergi*, Cairo, shape of 3 bursae copulatrices and 2 ♂ copulatory organs. 75. *C. costulatus*, Liberia: reproductive system; maximum shell diameter 4.9 mm, height 1.3 mm, 3⅔ whorls.

Gyraulus costulatus (Krauss, 1848)

Planorbis costulatus Krauss, 1848: 83, pl. 5, fig. 3 (Umgeni Valley, Natal).

Material—Liberia, five specs.

Shell—The shell is small- to medium-sized, scarcely reaching 5 mm in diameter and of moderate height (1.3 mm). Three and two thirds whorls increase rapidly. The periphery is angled, with a small fringe of periostracum. The surface is glossy, with regular costae in the direction of the growth lines.

Animal—The animal is uniformly light grey. The mantle has many well-defined small pigmented areas. The kidney has some tiny septa which, however, do not render its margins undulate. An intestinal loop is present. The entire reproductive system (Fig. 75) is delicate and slender: the ovotestis is very small.

The spermoviduct is long and slender. The seminal vesicle is inconspicuous. The albumen gland is composed of few long acini. The bursa copulatrix is tiny and is of an elongate club shape or tapering. The sperm duct is extremely narrow. The prostate gland bears 5 to 8 diverticula, which are irregular in shape and arrangement, the most distal one not touching the bursa copulatrix as in all Palaearctic species, but distant from it. The ♂ copulatory organ is of the normal form, but very short, scarcely exceeding 1 mm in length. The penis sheath is approximately the same length as the preputium or is slightly longer. The proximal end of the penis sheath does not reach the vagina in fully extended animals.

Remarks—The anatomy of this widely distributed tropical and southern African species

has been well known since various authors have dealt with it (Fraga de Azevedo *et al.,* 1961; Wright, 1963; Brown, 1965). A particularly comprehensive study has at the same time shown that there is a South African species resembling *Gyraulus costulatus* in many details, but clearly separated (Brown & van Eeden, 1969).

A comparison of the two African species, *Gyraulus costulatus* and *G. connollyi* with Palaearctic species shows several striking deviations from character states usually seen in the genus, namely the extremely small ovotestis, the tiny seminal vesicle, the very narrow sperm duct, the number of prostate diverticula that is by far lower (in Ethiopia no more than three, according to Brown, 1965), and the long distance between the most distal diverticulum and the bursa copulatrix. These character states, evidently commonly derived in *G. costulatus* and *G. connollyi,* strongly suggest the existence in Africa of a separate subgenus. Bourguignat (1883: 99) has established a genus *Caillaudia* with the type-species *G. angulata* Bourguignat. *G. angulata* is commonly accepted as a junior synonym of *P. costulatus.* Thus *Caillaudia* is available as a subgenus name for at least the two African species mentioned above.

Gyraulus convexiusculus (Hutton, 1849)

Planorbis convexiusculus Hutton, 1849: 657 (Candahar, Afghanistan).

Hutton's notes on habitats begin with ''Occurs plentifully at Candahar in tanks.'' Localities further listed by him are Quettah, Kojuck Pass, river Helmud at Girishk (all in Afghanistan) and, furthermore, the Gangetic provinces, at Tope Chancey, Pinjore below Simla. I consider Candahar the type-locality.

Material—Sayedabad, 3 specs. (unrelaxed); Gawargin (both Afghanistan), 2 specs. (unrelaxed), Mauritius, 3 specs. (named *G. mauritianus* (Morelet) by G. Mandahl-Barth) (unrelaxed); Bangalore, 6 specs. (unrelaxed); Bharatpur (both India), 4 specs. (unrelaxed); Thailand, 2 localities: 4 + 4 individuals (unrelaxed); further alcohol material was seen from Ceylon, but authorities of the Nat. Hist. Mus. Vienna did not permit dissection.

Shell (Fig. 76)—The shell is small- to medium-sized, 4 to 5 mm in diameter and relatively high (1.2 to 1.8 mm). Three and a half to 3¾ whorls increase rapidly. The umbilicus on the upper side is deep, on the under side shallow. The sutures are not very deep. The

last whorl is slightly deflected. The periphery is rounded or angled, sometimes with a fringe of periostracum. The surface is smooth and glossy, without reticulate sculpture. The color is light to dark corneous.

Animal—The animal is light to very dark grey. The mantle has a distinct pigmentation pattern, in intensity varying from very dark (Sayedabad, Mauritius) to light (Gawargin, Bangalore, Thailand). The kidney has straight margins. An intestinal loop is absent or present. The bursa copulatrix is small, spherical or elongate, its duct in most individuals being wide and not distinctly set off; the duct is as wide as the bursa itself (Fig. 77). The prostate gland bears 10 to 15 ($\bar{x}$ = 13.1 ± 1.7) (in Bangalore 20–24) closely spaced and regularly shaped diverticula, which are occasionally bifid. The vas deferens is as narrow as in most species. The ♂ copulatory organ is of the usual shape and 1–2 mm long. The penis sheath is as long or slightly longer than the preputium. Preputial pilasters are present. The penis tip has a thickening, with the penis pore in varying positions, in two individuals from Thailand virtually terminal (Fig. 78D), in the other ones subterminal, in the distal half of the thickening or near its middle.

Remarks—I have not seen the full range of characters in the few (unrelaxed) individuals I had available and better knowledge of variation will require study of additional material. Original material of Hutton's collection was to be found neither in ZSI, Calcutta, nor in BMNH, London. Annandale & Prashad (1919: 53) figured *G. convexiusculus* from Quetta, one of the localities indicated in Hutton's description. Their shell (Annandale & Prashad, 1919, fig. 7B) measures about 10 mm in maximum diameter, whereas Hutton (probably measuring one of the largest individuals, as usual at that time) speaks of 6.25 mm (''¼ of an inch''). The differences are striking, and the question may be raised again, whether Annandale & Prashad examined *Planorbis nanus* Sowerby, as has been suggested with their ''*G. euphraticus.*'' Starmühlner (1974: 168–171) figured organs of a snail from Ceylon, which is evidently conspecific with those anatomically examined in the present study. The shape and proportions of the ♂ copulatory organ as well as the narrow width of the vas deferens agree with those observed by me.

A more flattened and strongly angled form, usually considered *Gyraulus convexiusculus* ''var. *compressus* Hutton,'' has not been ex-
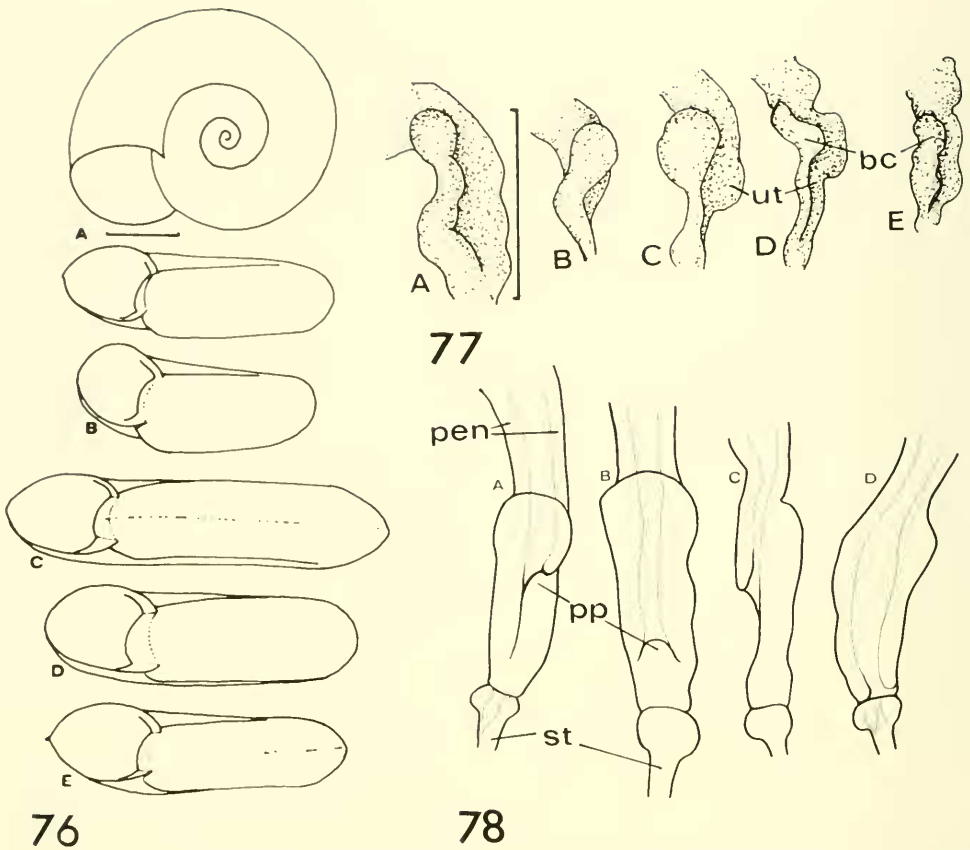
FIGS. 76–78. *G. convexiusculus.* 76. Variation in shell shape. A—Thailand (SMF 193 798); B—Thailand (SMF 197 350/15); C—Bangalore; D—Sayedabad; E—Gawargin. 77. Variation in shape of bursa copulatrix. A—Sayedabad (M 297); B, C—Gawargin (M 298); D—Bangalore; E—Thailand (SMF 193 798). 78. Variation in penis tip and position of penis pore. A—Gawargin (M 298); B—Sayedabad (M 297); C—Bangalore (M 299); D—Thailand (SMF 193 798).

amined anatomically. Their affinity can, thus, not yet be judged.

Character states of the reproductive system studied from Bangalore (India) are in good accordance with Baker's (1945, pl. 19, fig. 2) drawing of a specimen from Calcutta. Congruence even includes the number of prostate diverticula (23), which, as seen in the present study, is higher in Bangalore (20–24) than in Afghanistan (12–15) and Thailand (10–14). The data are, however, too restricted to generalize.

Gyraulus chinensis (Dunker, 1848)

Planorbis chinensis Dunker, 1848: 41 (Hong Kong).

Material—Hong Kong, 13 specs. (unrelaxed).

Shell (Fig. 79)—The shell is small- to medium-sized, 3.5–4 mm in maximum diameter and 1.2–1.3 mm in height. Three and three quarter whorls increase rapidly in width. The last whorl is not or slightly deflected. The periphery is rounded to moderately angled. A small periostracal fringe is present on some of the 28 specimens available from this population. The surface is not glossy, with growth lines irregular and pronounced. Fine spiral striae are present in most individuals. The colour is light to brownish-corneous.

Animal—The animal is light grey, the cephalopedal mass with small scattered black patches. There is a distinct pattern in the
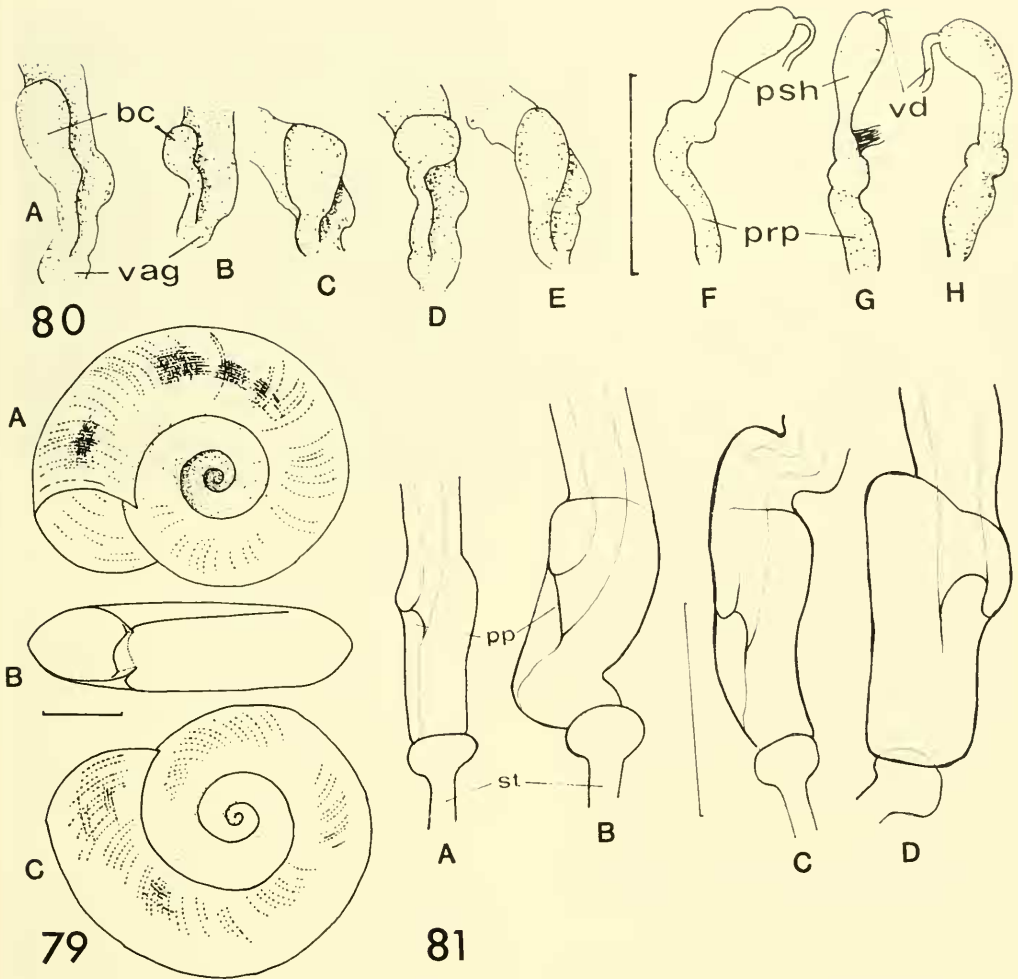
FIGS. 79–81. *G. chinensis*, Hong Kong. 79. Shell (SMF 246 321). 80. Variation in shape of bursa copulatrix and ♂ copulatory organ (SMF 246 322 and M 300). 81. Variation in shape of penis tip and position of penis pore (M 300). Scale = 0.1 mm.

mantle pigmentation (Fig. 12). The kidney margins are straight. An intestinal loop is present. The seminal vesicle is bulbous to slightly spinous. The bursa copulatrix (Fig. 80) is elongate or spherical club-shaped and sometimes large. The bursa duct is as wide as the vagina. The prostate gland bears 11 to 15 closely spaced diverticula. The vas deferens is equally narrow over its full length. The ♂ copulatory organ has the usual shape (Fig. 80) and is between 1 and 2 mm long. Preputial pilasters are present. The penis sheath is slightly longer than the preputium. The penis has a distal thickening, in which the penis pore is situated laterally at various sites (Fig. 81).

Remarks—Dunker's original material could be located neither in the Zoological Museum of Humboldt-University, Berlin (personal communication, Dr. R. Kilias) nor in BMNH, London. According to Dunker's description. snails in the type-series reached 4.75 mm in diameter and 1.15 mm in height, which is only slightly larger than in the present sample. The animals examined correspond to the original description except for the weak spiral striation that is not mentioned by Dunker, probably due to his poor optics.
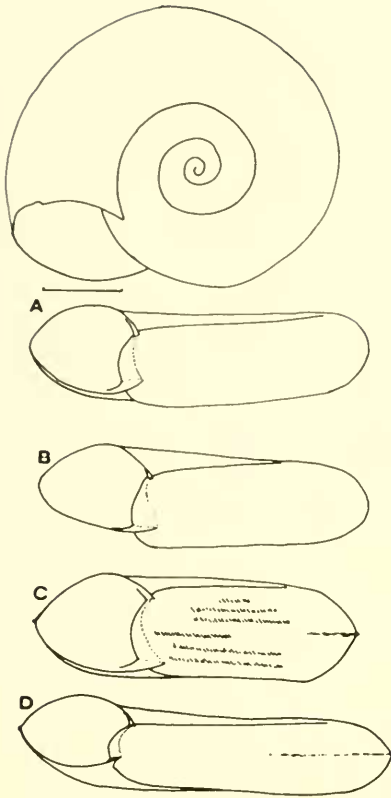
FIG. 82. *G. spirillus*, variation in shell shape. A—Onna-son (ANSP A453); B—Chongpyong (SMF 246 323); C—Kunsan (SMF 246 324); D—Taiwan (SMF 246 325).

FIG. 83. *G. spirillus*, Taiwan; shell surface on upper side and periphery. SEM. Scale = 0.01 mm.

Gyraulus spirillus (Gould, 1859)

Planorbis spirillus Gould, 1859: 40 (Ousima; =Amami-O-Shima, Ryukyu Islands, appr. 28°08′N, 129°19′E).

Material—Motobu-cho (Okinawa; as the locality nearest to Ryukyu-Islands), 5 specs. (unrelaxed); Taiwan, 60 specs. (20 of which unrelaxed); Korea: Chongpyong, 15 specs.; Kaejong, 5 specs.; Kunsan, 8 specs.

Shell (Fig. 82)—The shell is small to medium in size, rarely exceeding 5 mm in diameter and variable in height: rather flat, 1.2 to 1.4 mm in height (Fig. 85, lines 8 and 10), or less flat, 1.3 to 1.5 mm in height (lines 3 and 4). Three and a half to 4½ whorls, slowly (Taiwan) or more rapidly (other localities) increasing in size. The last whorl is more or less deflected. The periphery is angled, usually with a distinct fringe of periostracum. The

surface is smooth (Fig. 83) (Taiwan. Only one of several hundred shells from a laboratory stock had clear spiral striation!) or with reticulate sculpture. Spiral striae are faint to pronounced; in the latter case the surface has periostracal lamellae on growth lines, protruding in spiral rows (Fig. 82C) like the "hairs" of *Gyraulus albus* (Fig. 36C). The colour is light to brownish-corneous.

Animal—The animal is light grey, the cephalopedal mass being uniformly light grey or with many small black dots. The mantle pigmentation has a distinct pattern. The seminal vesicle is bulbous or spinous. The bursa copulatrix is extremely variable (Fig. 84), from slender and tapering to spherical club-shaped. The bursa duct likewise varies from narrow to wide. The vagina is usually inflated. The prostate gland bears 11 to 21 (Taiwan) or 8 to 19 (Korea) closely spaced diverticula (Table 6). The diverticula are two-branched. The vas deferens is narrow. The ♂ copulatory organ is of the usual shape, around 2 mm in length. The length of the penis sheath is 1.5 to 2 times that of the preputium. Pilasters are present in the latter. The penis tip is thickened, the position of the penis pore situated at various sites laterally in thickening.

Remarks—The lectotype of Gould's *Planorbis spirillus*, designated and figured by Johnson (1964, pl. 44, fig. 7), is very similar to the flat population from Taiwan or Kaejong; it carries some spiral striae ("lirae" in Gould's description).
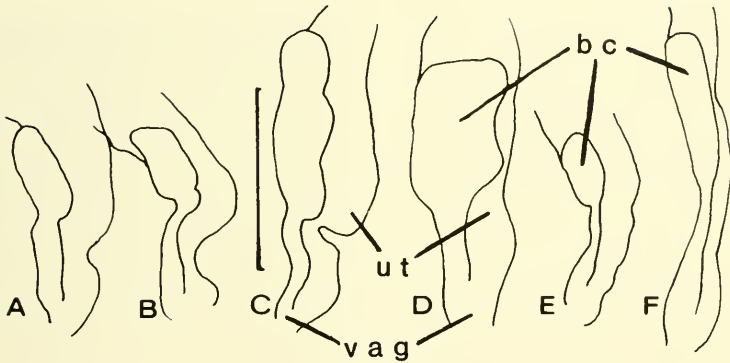
FIG. 84. *G. spirillus*, variation in shape of bursa copulatrix. A—Motobu-cho; B—Onna-son; C, D—Kunsan; E—Kaejong; F—Chongpyong. For Taiwanese specimens see Fig. 30.

Pace (1973: 79) figured the reproductive system of a species under this name from Taiwan, noting that the Taiwanese specimens have fewer than 20 prostate diverticula (cf. Table 6); his fig. 16 is completely in line with my observations. Pace, at the same time, poses the question again that has frequently been asked: are *Gyraulus spirillus, G. chinensis, G. convexiusculus,* and *G. euphraticus* forms of the same species? This question must be considered anew in the light of anatomical characters. As Table 6 shows, there are no essential differences between these four species in (1) mean numbers of prostate diverticula, (2) length of the copulatory organ, (3) ratio penis sheath : preputium. Moreover the shapes of the bursa copulatrix and a usually wide bursa duct as well as the penis tip do not show differences so consistent that species discrimination could be based on them. Nevertheless essential differences in shell characters exist, as Rensch (1934: 210–211) already pointed out. He expressed the height of the last whorl in its middle as a percentage of the maximum diameter, stating (translated): "In 24 typical *euphraticus* this percentage was 16.9–23.0%, mean 20.3%, in 57 typical *convexiusculus,* on the other hand, it was 21.9–35.5%, mean 27.4%." My own measurements of *G. euphraticus* from southern Iran yielded results similar to Rensch's (Figs. 85, 88). It is interesting to note that the other extremely flat shells of the group in question occur at the other end of the Asiatic continent: in Taiwan and Korea (Fig. 85, lines 9 and 10). Both the Iranian and the Taiwanese snails have smooth shells

without spiral striation, and it would be difficult to tell one from another, if the Taiwanese shells did not regularly carry a tiny, but distinct, fringe of periostracum, which is always absent in *G. euphraticus*. In the whole southern Asiatic region between Iran and the Far East flat and smooth forms with anatomical features of this group seem to be unknown.

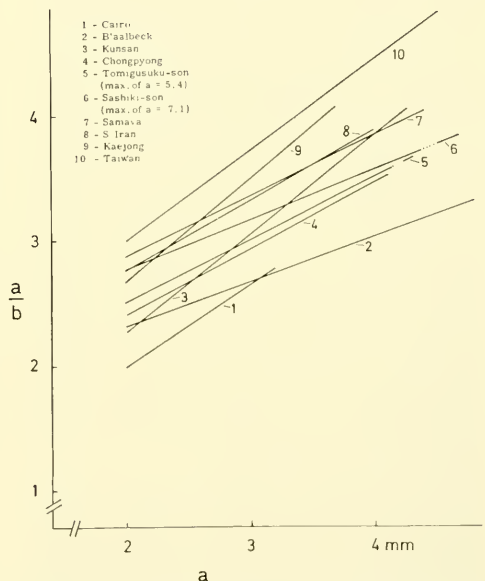In view of the slight differences in the group

FIG. 85. a/b plotted against a in samples from S and E Asia. The right upper end of the regression lines indicates the maximum value of a in the sample.
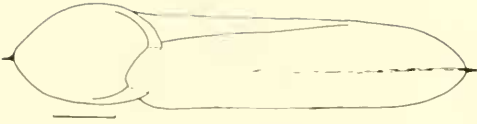
FIG. 86. *G. tokyoensis*, Sashiki-son, shell shape, apertural view.

it would seem reasonable to treat *Gyraulus euphraticus*, *G. convexiusculus*, *G. chinensis*, and *G. spirillus* as geographical races or sub-species of one species. One exception, how-ever, must probably be made. According to observations made by Dr. Mandahl-Barth and co-workers, Charlottenlund, *G. euphraticus* is sympatric with *G. convexiusculus* in Iran, where they are said to occur in the same water bodies (J. E. Jelnes, personal commu-nication, VIII-1977). This, of course, would be a strong argument for reproductive isolation between these groups and, thus, for sepa-rate species status of *G. euphraticus*. Hence, the group dealt with under the names of *G. convexiusculus*, *G. chinensis* and *G. spirillus* and perhaps some others form a separate network of races in south and east Asia. I want to apply the term Rassenkreis for this chain, as coined by Rensch (1929: 13, trans-lated): ''A Rassenkreis is a complex of geo-graphical races having immediately devel-oped from each other, geographically vicariating and showing unrestricted fertility between neighbouring races.'' We do not yet know whether *G. convexiusculus*, *G. chinen-sis* and *G. spirillus* are reproductively iso-lated. If they are reproductively isolated they would have to be considered sibling species. It would, in this case, not be justified to call the group of these three a superspecies, as defined by Mayr who replaced Rensch's ''Ar-tenkreis'' by this term: ''A superspecies con-sists of a monophyletic group of entirely or essentially allopatric species that are mor-phologically too different to be included in a single species'' (Mayr, 1963: 499). As shown above, morphological differences between the three groups are negligible.

A similar observation was made by Huben-dick (1951) who studied a great number of races of the lymnaeid snail *Radix auricularia* (L.), which have a distribution like *Gyraulus chinensis*, etc. The races, previously regard-ed as species, are defined on shell charac-ters, but show virtually no consistent differ-ences in anatomy. He found geographic

FIG. 87. *G. tokyoensis*, Tomigusuku-son, shell periphery with keel and weak reticulate sculpture; periostracum removed. SEM. Scale = 0.01 mm.

overlap of races with transitional forms oc-curring here and there. In western Burma and Assam, for example, the Indian race *R. a. rufescens* appears to grade into the Chinese race *R. a. swinhoei* (Hubendick, 1951: 154). In his discussion, Hubendick saw most rea-son for steering a middle course between the two alternatives: ''geographical races con-stituting one species'' or ''separate though closely related species, all of which . . . form one superspecies.'' Finally he apparently de-cided to speak of a superspecies, whereas I am tending to consider the *Gyraulus* widely distributed over south and east Asia mem-bers of one Rassenkreis. The reason is that the *Gyraulus* taxa called races are hardly dis-cernible from each other, even on the basis of shell characters. The oldest available name for this taxon is *G. chinensis* (Dunker).

In the material collected by G. M. Davis on Okinawa there are snails that I should iden-tify as *Gyraulus hiemantium*. They are almost congruent with Mori's figure of this species (Mori, 1938, pl. 15, fig. 9). Anatomically they do not show any substantial deviations.
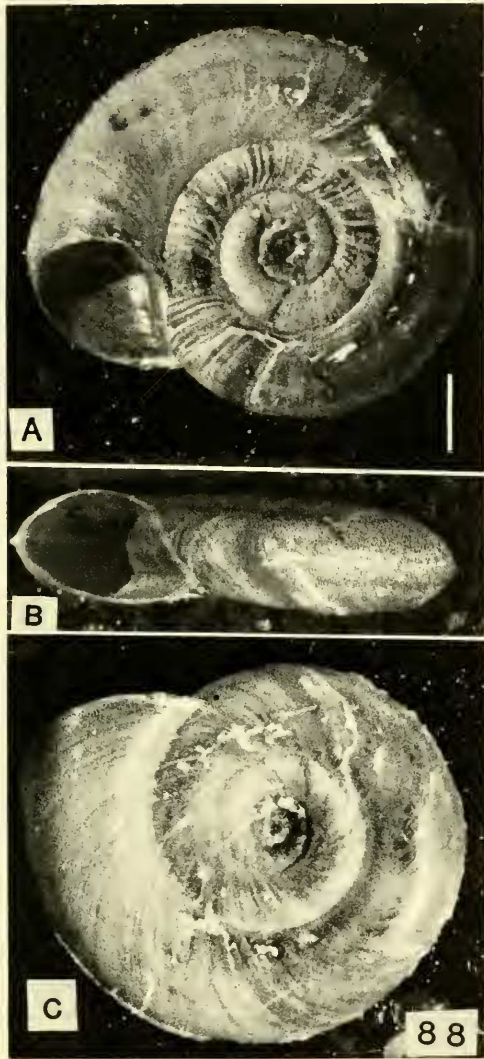
FIG. 88A–C.   *G. malayensis* n. sp., shell. Holotype (SMF 246 333).

FIG. 88D–F.   *G. malayensis* n. sp., shell. Paratype, Bukateja, Java (RMNH 9056/alcohol).

Should topotypes of *Planorbis hiemantium* Westerlund, 1883 from Hiroshima show the same characters, *G. hiemantium* may also be included in the *chinensis*-Rassenkreis as a very flat form of the race *G. ch. spirillus.*

Gyraulus tokyoensis (Mori, 1938)

Anisus (*Gyraulus*) *tokyoensis* Mori, 1938: 290 (Tokyo).

Material—Tomigusuku-son (Okinawa), 13 specs. (unrelaxed); Sashiki-son (Okinawa), 7 specs. (unrelaxed).

Shell (Fig. 86)—The shell is large, regularly exceeding 7 mm in diameter, relatively flat (2 mm in height), with 4¼ to 4½ rapidly increasing whorls. The last whorl is not or only slightly deflected. The periphery is distinctly angled and keeled (Fig. 87), carrying a wide fringe of periostracum (removed in Fig. 87 to show the keel). The surface shows weak reticulate sculpture. Anatomical characters (Table 6) are like those of *G. chinensis.*

Remarks—The lack of anatomical differences between *Gyraulus tokyoensis* and the *G. chinensis*-group suggests very close relationship. There are two reasons for maintaining *G. tokyoensis* as a separate species: (1) Size and a strongly keeled periphery distinguish *G. tokyoensis* from the *G. spirillus* race. Extreme forms within the *chinensis*-Rassenkreis differ from each other not to the same extent. (2) The two species live in the same region, e.g. on Okinawa. Here Davis & Yamaguchi (1969: 147) collected *Gyraulus* at 29 localities. Of these, 23 had *G. ch. spirillus* and 7 had *G. tokyoensis,* while at one site the two forms were found together. This could also mean that they are ecophenotypes of one species, but according to these authors
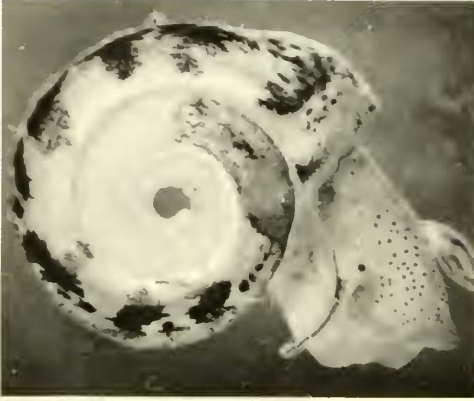
FIG. 89. *G. malayensis* n. sp., paratype, Kuala Lumpur, body pigmentation (shell removed).

"there was no gradation of *G. spirillus* into *G. tokyoensis*." Consequently *G. tokyoensis* apparently complies with the biospecies criterion of reproductive isolation from its closest relative.

Gyraulus malayensis Meier-Brook, n. sp.

Diagnosis—A species of the genus *Gyraulus* which differs from all known species by its extremely wide vas deferens, the penis sheath being not much wider than the vas deferens, and the penis pore being situated near the middle or in the proximal half of the penis.

Shell (Fig. 88A–F)—The shell is medium-sized to large, 3.5 to 6.5 mm in diameter, of varying height, the smaller snails being relatively high, 1 to 1.25 mm (Bukateja, Tasik Madu), the larger relatively flat, 1.2 to 1.55 mm (Kuala Lumpur). Three and three quarters to 5 whorls increase moderately fast. The periphery is rounded or slightly angled, angled forms having a wide fringe of periostracum (Kuala Lumpur). The last whorl is hardly deflected. The aperture is round to ovoid. The upper side is almost flat with shallow sutures. The under side is deeply concave with deep sutures. The surface is smooth to glossy, occasionally (Kuala Lumpur) carrying faint spiral striae. Growth lines are ± irregular. The colour is pale corneous.

Animal—The animal is light grey, the cephalopedal mass has distinct black spots (Fig. 89). The mantle pigmentation shows a distinct pattern, either with large black areas (Fig. 89) or smaller patches like those in *Gyraulus chinensis* (Fig. 12). The pseudobranch is large.

The kidney margins are straight. An intestinal loop is present. Ovotestis, seminal vesicle, and albumen gland are of the usual size and form (Fig. 90). The female tract is long and narrow. The bursa copulatrix is elongate club-shaped. The bursa duct is long and relatively wide (about the width of the vagina). The vagina is slightly inflated. The free sperm duct is conspicuously long. The prostate gland bears 17 to 25 (Kuala Lumpur) or 21 to almost 30 (Tasik Madu, not exactly determined in contracted specimens) or 29 and 33 (Bukateja) diverticula, which are densely and regularly arranged. The vas deferens is equally wide throughout its length (Fig. 90, 91A–B); its width is 0.12 to 0.20 (Kuala Lumpur), 0.10 to 0.14 (Tasik Madu) or 0.08 to 0.11 mm (Bukateja). The penis sheath is not considerably wider than the vas deferens, its widest portion being 0.14 to 0.24 (Kuala Lumpur), 0.16 to 0.20 (Tasik Madu) or 0.14 to 0.16 mm (Bukateja) wide. The preputium is of the usual form. Preputial pilasters are present. The penis sheath is longer than the preputium: the ratio penis sheath : preputium in Kuala Lumpur is $\bar{x} = 1.5 \pm 0.4$ (n = 8); Tasik Madu (unrelaxed!) $\bar{x} = 1.8$, (n = 3); Bukateja (unrelaxed!) $\bar{x} = 1.5$ (n = 4). The penis gradually tapers from about the middle of its length. The penis pore lies near the middle of the penis length or in its proximal half (Fig. 91C). The stylet has the normal form.

Type-locality—Kuala Lumpur (Malaysia), 5 km from the city, large abandoned tin-mining pool. On grass and *Eichhornia*. J. K. Lie legit, VI-1973.

Holotype (Fig. 88A)—6.1 mm in diameter, 1.5 mm high; a:b = 4.6:1.25 mm, 4⅞ whorls. Deposited in SMF 246 333/1.

Paratypes—SMF 246 334/4 and 246 326 (microscopical preparation); RMNH, Leiden (alcohol), no. 9055/4 from Kuala Lumpur. SMF 246 335/3 from Tasik Madu, N Bali: Lovina Beach, legit K. Y. T. Tjhen, VI-1976, RMNH Leiden (alcohol) no. 9056/2 from Bukateja, south-central Java, Tjhen legit, VI-1976 (Fig. 88B)

Additional paratypes are in the author's collection. Material examined anatomically: Kuala Lumpur (Malaysia) 11 specs., Tasik Madu (Bali) 4 specs. (unrelaxed); Bukateja (Java) 4 specs. (unrelaxed).

Conchologically, this new species appears to fall in the range of variation of what has usually been called *Gyraulus convexiusculus*. The expert for Indonesian mollusks, Dr. van der Feen van Benthem-Jutting of Domburg
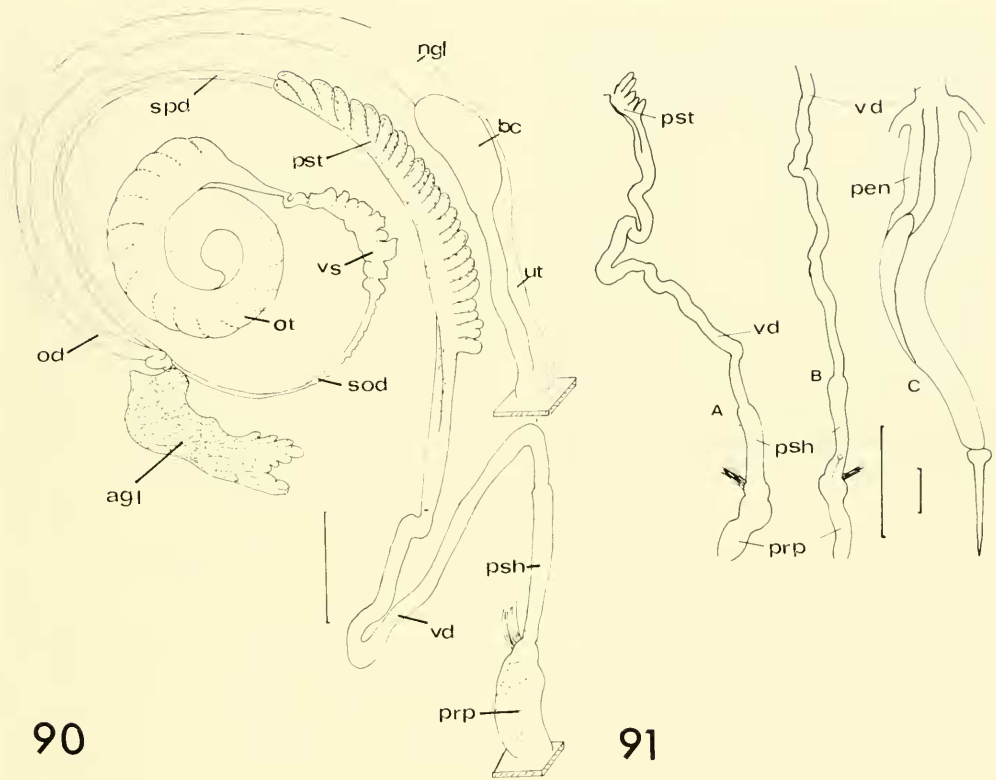
FIGS. 90–91. *G. malayensis* n. sp. 90. Paratype, Kuala Lumpur, reproductive system (SMF 246 326). 91. Paratypes. A, B—♂ copulatory organs with vas deferens from Tasik Madu, Bali and Bukateja, Java. C—penis of a specimen from Tasik.

(Netherlands), was kind enough to check the shells of the Javanese and Balinesian samples and to give me her opinion (*in litt.* 22-XI-1976), before I began to study their anatomy. She used to attribute the name *G. convexiusculus* to snails of this form. In her monograph of Javanese mollusks (van Benthem-Jutting, 1956: 463) she mentions only two *Gyraulus* species: *G. convexiusculus* and *G. terraesacrae* Rensch. *G. terraesacrae* is a tiny species not exceeding 2.2 mm in diameter and is probably a separate species. Whether the Indonesian material in the various collections named *G. convexiusculus* really belongs to this species or rather to *G. malayensis* n. sp. cannot be judged without extensive anatomical studies. It is hoped that future studies will also reveal reliable conchological differences between *G. chinensis* and *G. malayensis* n. sp.

Most characters of the animal of the new species shared by *Gyraulus chinensis* are symplesiomorphous within the subgenus *Gyraulus* and thus of little value, but the distinct pattern of mantle pigmentation and perhaps also the relatively wide bursa duct are synapomorphous within the subgenus. These synapomorphies indicate close relationship between *G. chinensis* and *G. malayensis*. Moreover, there is a high probability that in Indo-China there has never been any other taxon from which *G. malayensis* could have split off than the parent species *G. chinensis*. And the presence of *G. malayensis* in Malaysia and in Indonesia strongly suggests that isolation took place somewhere in or near the Malayan peninsula.

Reproductive isolation between *Gyraulus chinensis* and *G. malayensis* is not only understandable because of the fundamental difference in the copulatory organs but also because their geographical ranges overlap in at least one region: a sample from Malacca, approximately 120 km SSE of Kuala Lumpur,

FIG. 92. *G. eugyne* n. sp., holotype (NHRM Stockholm 2198).

recently received from Mr. Sigurdsson, contained the species common in S Asia: *G. chinensis*. From this finding it is probable that the two species are sympatric in Malaysia. One of the most exciting questions now is whether they are sympatric also in Sumatra, Java, Bali, and Borneo, which according to Rensch (1936: 267) and other zoogeographers (de Lattin, 1967, fig. 58; Illies, 1971: 53–54) were separated from Java, Sumatra and the continent at the end of the Pleistocene.

Gyraulus eugyne Meier-Brook, n. sp.

Diagnosis—A species of the genus *Gyraulus* which differs from all known species by its extraordinarily inflated bursa copulatrix.

Shell (Figs. 92, 93)—The shell is medium-sized to relatively large and has 3¾ to 4¼ whorls with the periphery rounded. The last whorl is deflected. The aperture is slightly oblique and round to ovoid. The shell is deeply umbilicate on the upper side and slightly concave on the under side. Fine growth lines are present. The surface is almost smooth, with at most a few faint spiral striae. The sutures are deep and the whorls are rounded laterally.

Animal—The cephalopedal mass is almost dark grey. The mantle pigmentation consists of a weak pattern, similar to that in *Gyraulus acronicus*. In the reproductive system of three paratypes the prostate gland had 17, 15 and

14 diverticula; the ♂ copulatory organ (1.8, 3.4 and 2.2 mm long) is of the ordinary type, the length ratio penis sheath : preputium (1.4, 1.6, 1.9) being in the range of *G. acronicus*. The penis pore has not been located exactly but seems to be at the base of the bulbous thickening. The bursa copulatrix in all three individuals showed enormous inflation, comparable to the "spherical tadpole type" in some *Planorbis*-species (cf. Meier-Brook, 1976c), which has to this extent never been observed in any other *Gyraulus* species. This amount of inflation cannot solely be caused by recent copulation. It greatly exceeds the amount observed in freshly mated individuals of other species. Moreover, the characteristic orange color of the bursa contents, as is usually seen in freshly mated individuals, was absent here.

Type-locality—Inner Mongolia ("Läger XI" Honnen-tjaggan-tschollogol; Sven Hedin-Expedition, 1927).

Holotype—NHRM Stockholm no. 2198 (Fig. 92); 5.9 mm maximum diameter, 4⅛ whorls; 2.3 mm height; a:b = 4.25:1.55 mm.

Paratype no. 1—6.2 mm diameter; 2.1 mm height; a:b = 4.5:1.35; Paratype no. 2—5.7 mm diameter; 2.2 mm height; a:b = 4.15:1.5; Paratype no. 3—5.7 mm diameter; 2.2 mm height; a:b = 3.9:1.5 (Fig. 93); Paratype no. 4—5.6 mm diameter, 2.0 mm height; a:b = 4.1:1.5; Paratype no. 5—6.6 mm diameter; 2.1 mm height, a:b = 4.3:1.45.

Relationship—Conchologically, there is superficial resemblance between *Gyraulus eugyne* and *G. piscinarum*, both having a mean ratio a:b of 4.2:1.5 in adult specimens. Anatomically the size and shape of the bursa copulatrix (Figs. 71 and 94) also show some affinity. The mean number of prostate diverticula lies within the range of that in *G. piscinarum* and *G. chinensis* with subgroups, while shell characters are quite different from those in the latter species.

So far as we know, *Gyraulus piscinarum* has a restricted distribution in the Near East. Its occurrence, as an eastern race, in Mongolia, approximately 7000 km distant from the Near East, appears improbable. The shells could be compared with the east Siberian forms of *G. acronicus,* but the number of prostate diverticula does not fall in its range. However, close relationship with *G. acronicus* cannot be excluded. Of the many *Gyraulus* species described from China there is none that is conchologically similar except, perhaps, *G. zilchianus* Yen. As long as the
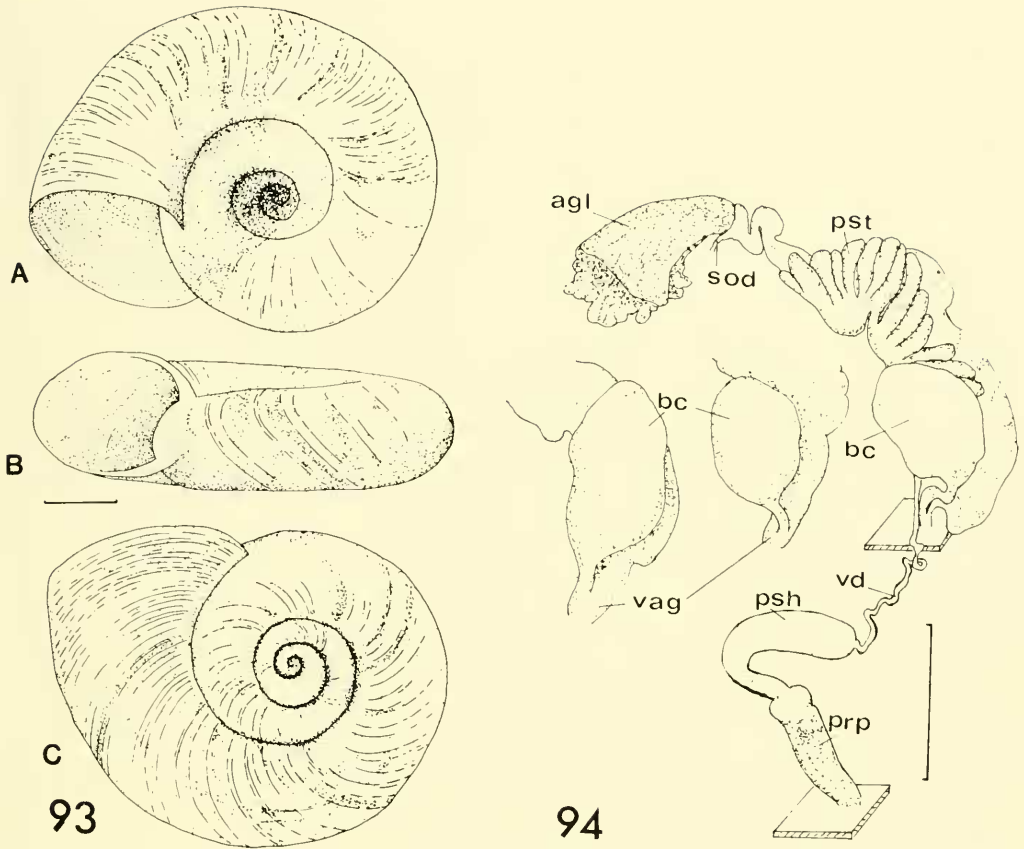
FIGS. 93–94   G. eugyne n. sp. 93. Paratype no. 3; (NHRMS 2198). 94. Reproductive system, including shapes of two further bursae copulatrices. Paratypes (NHRMS 2198).

chance of studying Chinese material anatomically is virtually zero (my attempt to collect in Soochow, the type-locality of G. zilchianus, was obstructed) I dare not identify the only anatomically known species from China with a conchologically defined species from a locality more than 1300 km distant. Thus, I prefer to run the risk of creating another synonym in order to avoid misidentification of this species.

Concluding Remarks on South Asiatic Species

Our knowledge of anatomical characters in Gyraulus species must still be called sporadic with regard to the dimensions and geomorphological heterogeneity of the southern part of Asia. We may state that there is one Rassenkreis extending from Middle to Far East: G. chinensis. There is also no doubt that the Near East harbours at least two species clearly separated from G. chinensis, viz. G. piscinarum and G. ehrenbergi. There is probably also a third one, G. euphraticus. In the Far East there is one taxon considered here as a separate species though with close affinity to G. chinensis: G. tokyoensis. Possibly Japan is inhabited by more than these two species, apart from the endemic species of Lake Biwa. It is, of course, premature to claim that in the entire south Asiatic region any Gyraulus must be a member of the Rassenkreis of G. chinensis. Conchological variation, e.g. in the Chinese Gyraulus fauna (Yen, 1939, pl. 6, figs. 1–8), suggests that there are a few more separate species, as the discovery of G. eugyne n. sp. from Inner Mongolia implies. No further conclusions, however, are reason-

able without anatomical studies of more material from this region.

Although I am far from having full knowledge of the species inhabiting the Orient, I provide a provisional key. Users should be aware of its incompleteness and of possible weaknesses, e.g. a sure distinction between *Gyraulus chinensis* and *G. euphraticus*. As

pointed out above there are forms of *G. chinensis*, such as the Taiwanese population dealt with here under the name *G. spirillus*, that are almost indistinguishable from *G. euphraticus*. Unfortunately there are not even anatomical characters constant enough to support a decision, so that only geographical distribution offers help.

A Provisional Key to the *Gyraulus* Species Inhabiting
Continental Southwest, South and East Asia

1A. Mantle pigmentation diffuse, without a distinct pattern and poor in contrast, underside of shell flat or slightly concave or convex, upper side deeply concave, aperture ± oblique; 3 to 4 whorls rapidly increasing, diameter 5 to 6 mm, periphery rounded; surface dull . . . . *G. piscinarum*
1B. Mantle pigmentation with a distinct pattern rich in contrast, though sometimes weakly developed (± pale), surface ± shiny 2
2A. Vas deferens wide, not much narrower than penis sheath, not well set off against it; penis tapering towards its tip; penis pore in middle or proximal half of penis . . . . . .
. . . . *G. malayensis*
2B. Vas deferens slender, considerably narrower than penis sheath, always well set off against it; penis with ± distinct distal thickening with the penis pore in or close to it
. 3
3A. Shell scarcely >4 mm in diameter, relatively high: 1.3 mm; 3½ whorls very rapidly increasing, periphery slightly angled, with a small fringe of periostracum; animal poor in pigment, but pattern, though poor in contrast, discernible on mantle . . . *G. ehrenbergi*
3B. Shell larger, >4 mm in diameter, mantle pigmentation rich in contrast 4
4A. Bursa copulatrix much inflated (balloon-like), wider than uterus, bursa duct narrow; shell 5 to 6 mm in diameter, scarcely concave on under side, deeply concave on upper side; about 4 whorls rapidly increasing, periphery rounded . . . . *G. eugyne*
4B. Bursa copulatrix ± elongate, not wider than uterus, bursa duct ± wide; shell periphery often angled 5
5A. Shell large, >6 to 7 mm in diameter, 4¼ to 4½ whorls rapidly increasing, periphery keeled, with a conspicuous fringe of periostracum . . . . *G. tokyoensis*
5B. Shell small, usually < 5 to 6 mm in diameter, periphery rounded or angled 6
6A. Shell flat, height at most 23% of diameter; surface glossy, spiral striation absent . .
. . . . *G. euphraticus* (? = *G. hebraicus*?)
6B. Shell usually biconcave, height usually >25% of diameter, periphery rounded or angled, fringe of periostracum often present, surface usually glossy; fine spiral striation sometimes present . . . . *G. chinensis*

SPECIES OF ANCIENT LAKES

Molluscs are one of those groups of organisms that first drew biologists' attention to highly distinctive endemic taxa in lakes of Tertiary origin. Examples of lakes with well known endemic molluscan faunas are Lake Tanganyika, Lake Titicaca, Lake Biwa, Lake Baikal, and Lake Ohrid. Regarding the *Planorbis*-tribe (sensu Hubendick, 1955), en-

demic taxa have been described from the three last mentioned lakes, all situated in the Palaearctic region. The genus *Choanomphalus* was established as the first representative of ancient lake planorbids (Gerstfeldt, 1859). A striking character of this genus is its pseudo-dextrality caused by hyperstrophy. Subsequently, the first planorbid snail endemic to Lake Ohrid was described as *Planorbis (Gyrorbis) macedonicus* by Sturany

(1894) who pointed out its great similarity to *Choanomphalus*. Finally, a new species was discovered in Lake Biwa and relegated to *Choanomphalus* (Preston, 1916). The possibility that a peculiar planorbid genus was common to three ancient lakes so far distant from one another opened up exciting aspects as to the origin and evolution of such a group. Studies on the Baikalian snails revealed that *Choanomphalus* is anatomically distinct from *Gyraulus*, because of the acquisition of a distal accessory gland complex at the male copulatory organ, which gives the genus a unique status in the family (Hubendick, 1954, 1955). There are other features, however, such as the penial stylet, that leave no doubt that it is the group around *Gyraulus* that must have given rise to the seven Baikalian *Choanomphalus* species. Surprisingly, Lake Baikal has no endemic species of the genus *Gyraulus* itself. The *Gyraulus* species inhabiting the lake has been identified by previous authors as *G. gredleri* (=*G. acronicus*) (Kozhov, 1963: 159). Unfortunately, no material from Lake Baikal was available for my anatomical studies.

Species of *Gyraulus* from Lake Ohrid have been examined thoroughly as regards morphology (Hubendick & Radoman, 1959). There are four species of *Gyraulus* in the Ohrid basin similar to each other and strikingly distinct from European species outside the Ohrid basin. A fifth species resembles the usual *Gyraulus* species, but has been described as *G. albidus* (Radoman, 1953). The first of the four unusual Ohrid species relegated to a new subgenus, *Carinogyraulus*, was *G. trapezoides* (Polinski, 1929). A new species described from neighbouring Lake Prespa (*G. stankovici*) was considered to be *Carinogyraulus* (Hadžišče, 1953). No doubt the remaining three species of the Ohrid basin, *G. lychnidicus* Hesse, *G. crenophilus,* and *G. fontinalis* (but not including *G. albidus*) can be united in this subgenus. Probably a fifth species, *G. paradoxus* Sturany, 1894, belongs here. Hubendick & Radoman's (1959) information was so ample that further investigations on Ohrid species did not appear urgent, and my studies are thus restricted to the dissection of one individual of *G. lychnidicus* (see below).

The species described as *Choanomphalus japonicus* and *Gyraulus biwaensis* by Preston (1916) have not been previously examined anatomically. Information on these forms is given below.
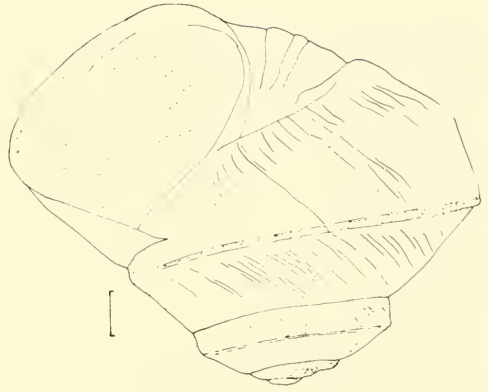
FIG. 95. *G. lychnidicus*, Lake Ohrid, shell (in coll. W. Rähle). Scale = 1 mm.

Gyraulus lychnidicus Hesse, 1928

Gyraulus lychnidicus Hesse, 1928: 6, pl. 1, fig. 4a–c (Lake Ohrid).

Material—One spec. (unrelaxed) collected by W. Rähle on the shore of L. Ohrid between Trpejica and Sveti Zaum (shell in coll. Rähle).

Shell (Fig. 95)—The shell is pseudo-dextral, very large compared with other *Gyraulus* species, 10 mm in width and 8 mm in height; the whorls are angled and keeled, first at their greatest diameter, secondly and more weakly on their highest elevation forming the crest of the funnel-like depression (umbilicus). *G. lychnidicus* is a thick-shelled species.

Animal—The animal is light to dark grey on the head-foot complex; the mantle is nearly uniformly black, both on the kidney and on both sides of it. Strong pigmentation is also present on the alimentary tract except the digestive gland where it is merely pale. Of the reproductive organs also the preputium, the vagina, and the bursa copulatrix are covered by dense pigmentation in the individual dissected, while the vas deferens and the spermoviduct including the seminal vesicle are completely devoid of pigment. All other parts of this system show scattered pigmentation.

The reproductive system (Fig. 96) is characterized by a conspicuous seminal vesicle with bulbous coiling, a prostate gland in which more than 60 diverticula are arranged in several rows, and a relatively wide vas deferens, reaching more than 0.2 mm in width. The pe-
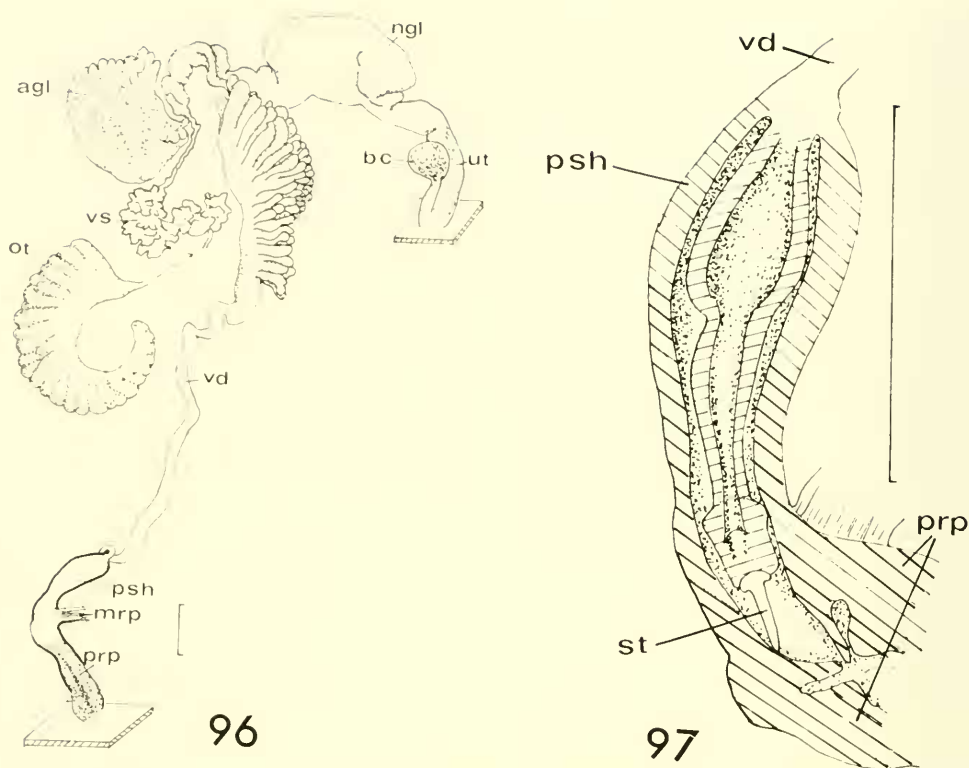
FIGS. 96–97. *G. lychnidicus,* Lake Ohrid. 96. Reproductive system (M 270). 97. Proximal portion of ♂ copulatory organ.

nis sheath and preputium in this contracted individual are of equal length, viz. 1.8 mm, and of usual width, 0.5–0.6 mm. The penis (Fig. 97) has a bulbous thickening, in the middle of which the penis pore is situated.

The radula (Fig. 98), as already stated by Hubendick & Radoman (1959), has unicuspid teeth (except in some marginals), as in *Gyraulus crenophilus* Hubendick & Radoman, *G. fontinalis* Hubendick & Radoman, and *G. trapezoides* Polinski.

Remarks—While Hubendick & Radoman's (1959) fig. 21 might suggest that in the prostate gland the diverticula are arranged like the rays in a fan, I found that in the individual dissected the diverticula emerged from the whole length of the prostate duct although in cross sections one would see an arrangement as in a fan. Finding the penis pore closer to the penis tip is in contrast with Hubendick & Radoman's (1959) statement that it "normally seems to be located well above the

middle of the penis in large sized specimens."

Gyraulus stankovici Hadžišče, 1953

Gyraulus stankovici Hadžišče, 1953: 175, figs. 3–4 (Lake Prespa).

Material—One spec. (unrelaxed) dredged by W. Rähle in Lake Prespa, Macedonia, at Oteševo (7 June 1973); 12 specs. (poorly preserved) collected by W. Maassen at the same locality (May 1976).

Shell (Fig. 99)—The shell is pseudo-dextral, rather small, 3.8 mm maximum diameter, 1.3 mm high; the 3¼ whorls are provided with three strong keels: the first delimits the funnel (umbilicus) on the upper side; the second forms the periphery of a whorl; the third delimits the almost completely flat under side. At the site of the keels the shell is acutely angled so that it appears concave between keel 1 and 2 and between 2 and 3. *Gyraulus*

stankovici is not as thick-shelled as indicated for *G. lychnidicus*. The shell surface is coarse. Irregular growth marks and a faint spiral striation form a reticulate sculpture.

Animal—The animal is light grey on the head-foot complex, dark grey at the lateral margins of the kidney, almost black in the region of the reproductive organs on the right side, but nearly pigmentless in the remaining mantle parts. Rather dense pigmentation is present on most parts of the alimentary system.

The reproductive system as found in the one well preserved individual is shown in Fig. 100. It is too early to give a general description, but it can be said from examination of this specimen that the prostate diverticula are arranged in a single row and are few in number (here 14). The radula of several individuals examined shows characteristics intermediate between the usual *Gyraulus* type and the Ohrid species. A few central teeth are bicuspid, most are unicuspid and tend to elongate. The lateral teeth are mostly tricuspid, but the mesocone is usually enlarged, while the endocone has almost disappeared and the ectocone is greatly reduced (Fig. 101).

Gyraulus biwaensis (Preston, 1916)

Choanomphalus japonicus Preston, 1916: 160, pl. 9, figs. 2–2c (*non Planorbis compressus japonicus* v. Martens, 1867 [a *Gyraulus*]).

Choanomphalus japonicus perstriatulus Preston, 1916: 161, pl. 9, figs. 1–1c.

Planorbis (*Gyraulus*) *biwaensis* Preston, 1916: 161, pl. 9, figs. 3–3c.

Anisus (*Gyraulus*) *biwaensis,* Mori, 1938: 292, pl. 16, fig. 11a–f.

Gyraulus biwaensis, Kuroda, 1963: 22.

Material—Lake Biwa (Japan) at Eizan (10 extended specs. collected by H. D. Boeters on 19 February 1975); Lake Biwa at Oura (2 retracted specs. collected by T. Miura on 12 June 1975).

Shell (Fig. 102)—The shell is pseudo-dextral, but the spire is not considerably elevated above the last whorl. This thick-shelled (0.04 mm in periphery of the last whorl) species is relatively small: width 3–3.5, height 1.5–2 mm; apertural height 1.2–1.5 mm. There are usually three keels. The middle keel lies on the periphery and the upper and lower ones are about equidistant from it. The upper keel delimits the funnel leading to the deep umbilicus. The lower keel surrounds the more or
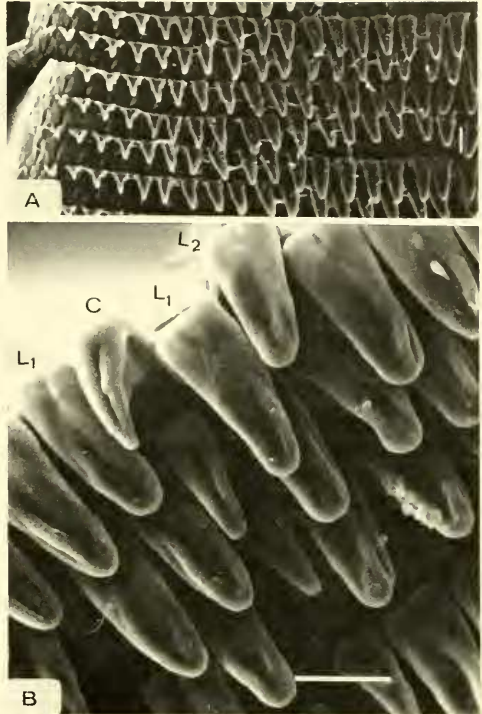
FIG. 98.   *G. lychnidicus,* Lake Ohrid, Parts of radula, with (A) lateral and marginal teeth and (B) central (C) and first lateral teeth (L). SEM. Scale = 0.01 mm.

less flat underside that is only interrupted by relatively deep sutures. There are usually three to five spiral striae between every two keels.

Animal—The animal is relatively uniformly pigmented. The head-foot complex is light grey, the mantle roof is similarly pigmented, as described for *Gyraulus lychnidicus* but not as dark. There is no pronounced pigment pattern.

The whorls are relatively short, wide and high; most organs are likewise short and wide (Fig. 103). This is the case with the albumen gland, the free sperm duct, the prostate gland (7–12 diverticula, $\bar{x} = 10.1 \pm 1.7$), the oviduct and uterus. The striking exception is made by the male copulatory organ that is— in its extended state—so long that its upper end nearly reaches the carrefour. The penis sheath is slightly longer (psh = 0.9–1.2 mm, $\bar{x} = 1.0 \pm 0.1$) than the preputium (prp = 0.75–1.05 mm, $\bar{x} = 1.0 \pm 0.1$) (psh:prp =
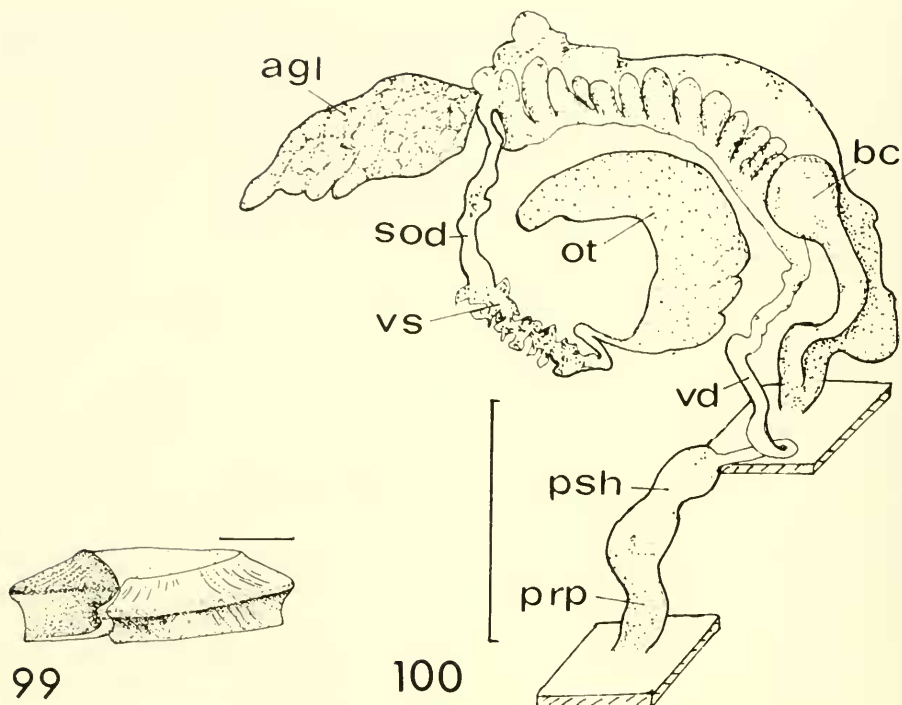
FIGS. 99–100.   *G. stankovici*, Lake Prespa. 99. Shell, apertural view. 100. Reproductive system (M 281).

1.1–1.3). The bulbous thickening of the penis tip is inconspicuous. The penis pore is situated in its upper half (Fig. 104). Preputial pilasters are well developed.
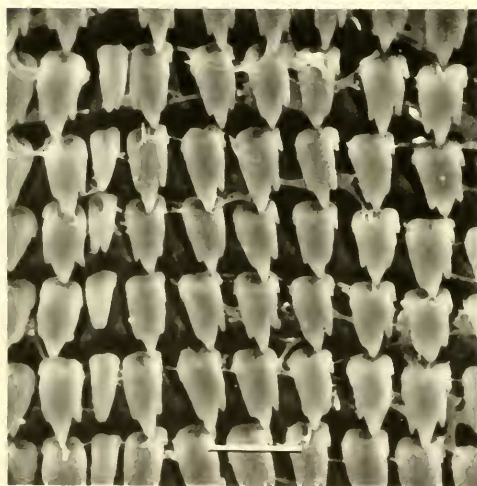
FIG. 101.   *G. stankovici*, Lake Prespa, central and lateral teeth of radula. SEM. Scale = 0.01 mm.

The radula formula is 13/14-1-13/14. The teeth are basically of the usual type in the genus (Fig. 105).

Remarks—The proportionally long ♂ copulatory organ gives *Gyraulus biwaensis* a unique position within the genus. This and the lack of a distinct pigment pattern make it unlikely that it has a common origin with the *G. chinensis* group. Thus these taxa do not appear very closely related. Its placement in the genus *Choanomphalus* has already been refuted by Mori (1938: 294) in a radula study, and by Kozhov (1963: 132–133) on conchological grounds. Anatomical study confirms this. The organization is even closer to the non-endemic group of *Gyraulus* than to the Macedonian endemic subgenus *Carinogyraulus* as the following considerations will demonstrate.

The marked multiserial arrangement of prostate diverticula, their great number, the unusual width of the vas deferens, and the unicuspid central and lateral teeth of the radula appear to be the character states common to the non-planispiral *Gyraulus* species of Lake Ohrid. Neither of these characteristics is found in *G. biwaensis* where, on the
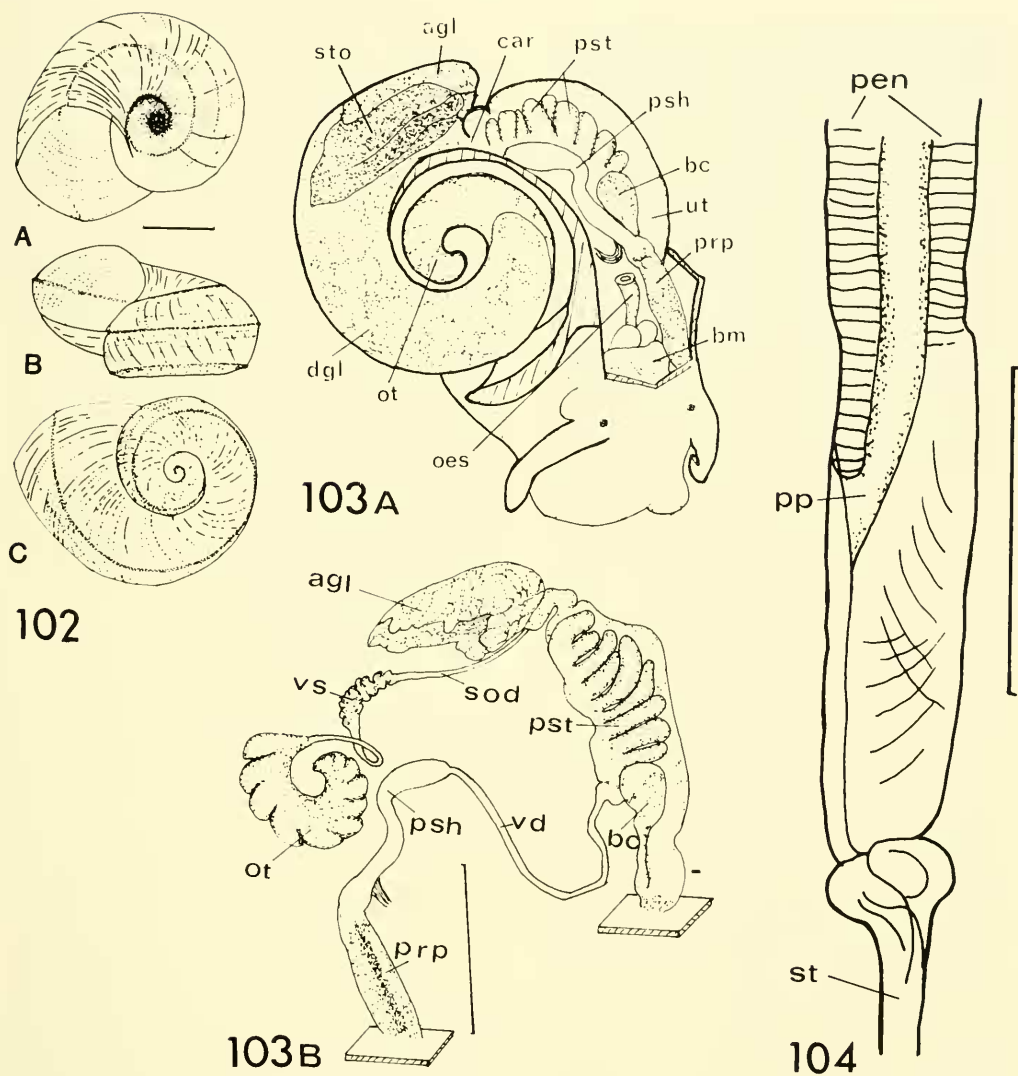
FIGS. 102–104.   G. biwaensis, Lake Biwa at Eizan. 102. Shell. 103A: Reproductive organs in situ demonstrating the relative length of the ♂ copulatory organ (mantle roof and esophagus removed); B: Reproductive system. 104. Penis tip. Scale = 0.1 mm.

contrary, the prostate diverticula are arranged uniserially and are relatively few in number. The vas deferens in G. biwaensis is as narrow as in G. albus and in any species outside Macedonia and the Malay Archipelago except G. parvus, where, as described above, the inferior half is largely thickened.

Nomenclature—The three names for this species, Choanomphalus japonicus, Choanomphalus japonicus perstriatulus, and Pla-

norbis biwaensis were introduced in the same publication. The first revising author, Mori (1938), stated that these are synonyms. He chose to use the name G. biwaensis. Kuroda (1963: 22) followed him, though pointing out that G. perstriatulus chosen by Preston as a subspecies name would have line priority. According to article 24 (a)(i) of the International Code of Zoological Nomenclature, Mori's choice of G. biwaensis must stand.

FIG. 105.   *G. biwaensis,* Lake Biwa, central and first lateral radula teeth. SEM. Scale = 0.01 mm.

Concluding Notes on the Ancient Lakes Species

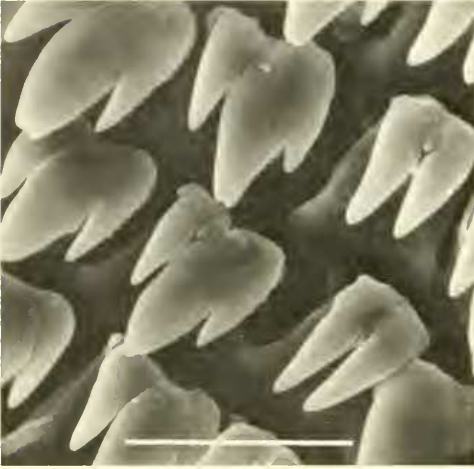The similarity of *Gyraulus* species from Lake Ohrid, Lake Prespa and Lake Biwa, that led conchologists to assume that they had a common origin, apparently is restricted to shell characters. Conchological features in common are the abandonment of planispiral growth and a tendency to form angles and keels. These character states appear to be unique in any planorbid genus and can be considered derived. As long as they were the only characters known for these species it would have been plausible to assume them to be *common* derived characters and to consider the four Ohridan species plus *G. stankovici* plus *G. biwaensis* to be synapomorphous in Hennig's sense. Anatomical differences show that the assertions based on conchology cannot be accepted.

The ancient lakes were, as today, large and it is probable that wave action selected for planorbids with shells hydrodynamically suited to such an environment, i.e. with more globose than planispiral shells, and with a trend towards thickening and reinforcing angles and keels. It is thus not surprising that shells with such attributes arose in geographically separated lakes by convergent evolution.

The conditions necessary for developing these shell forms was sufficient time in a stable habitat, i.e. where populations did not need to frequently adapt to changing environmental conditions, as is the case in virtually all inland waters that are—geologically speaking—ephemeral.

Similar phenomena can be observed in other groups of ancient lakes molluscs, where a general trend in forming angles, keels, sculptures and other reinforcing shell structures is obvious. Convergent evolution in these groups has partly led to shells of such a striking resemblance with marine groups that, for a long time, the Tanganykan endemic prosobranch snails were considered immediately derived from marine ancestors (Hubendick, 1952). To a lesser extent convergent evolution in various lakes has also been demonstrated in basommatophoran snails. A good example is the freshwater limpets *Acroloxus macedonicus* Hadžišče from Lake Ohrid, and *A. kobelti* (Dybowski) and *A. boettgerianus* (Lindholm) from Lake Baikal, which have radial ribs making them appear like small Siphonariidae.

After thorough anatomical examination, Hubendick (1960, 1969) concluded that the Ohridan and Baikalian *Acroloxus* species have evolved independently and that "evolution has obviously run parallelly in the two groups" (Hubendick, 1969: 66). It is interesting to state that also in the Acroloxidae a trend is visible towards reduction of radular cusp numbers. But according to Hubendick (1969: 66), "this process has resulted in mostly bicuspid laterals in the Baikal species and unicuspid laterals in the Ohrid species." As shown above, four of the five *Gyraulus* species in Lake Ohrid have unicuspid centrals and laterals. Since bicuspid centrals and tricuspid laterals are the rule not only throughout the genus but in the whole family Planorbidae as well, there can be no doubt about the direction evolution proceeded: somewhere in the Macedonian region a reduction of cusp numbers must once have taken place, and that *before* speciation within the Ohrid basin began (Fig. 106).

Concerning the fifth Ohridan species, *Gyraulus albidus,* it would seem that it has a different origin and closer relationship with *Gyraulus albus.* While Radoman (1953: 58) originally suggested that his species be conchologically and anatomically compared with *G. albus, G. laevis* and *G. gredleri,* in 1959 (Hubendick & Radoman, 1959: 239–243) he did not comment further on this aspect, and most recently (*in litt.* 2 February 1977) he expressed the opinion that *G. albidus* cannot

be separated from the group of Ohridan *Car-inogyraulus* species. I have specified the con-chological and anatomical features separat-ing *G. albidus* from the other Ohridan species above, and the decision on whether *G. albi-dus* is to be included in this group may de-pend on the width or narrowness of the scope of a subgenus. Until *G. albidus* can be ex-amined anew the question must remain open (Fig. 106). For now the subgenus *Carinogy-raulus* will include no more than the Ohridan species (except *G. albidus*) plus *G. stankovici* from Lake Prespa. The latter is included here mainly because of the obvious reduction seen in radula cusp numbers. This reduction and the short distance of Lake Prespa from Lake Ohrid make it improbable that *G. stankovici* and the four peculiar Ohrid species evolved independently. Because of the probable close ancestry of these species I assume that the conchological similarities likewise attest to a close relationship, i.e. were not derived by convergent evolution. The character state that distinguishes *G. stankovici* from the Ohridan forms is the uniserial arrangement of pros-tate diverticula and their low number. This evidence indicates that *G. stankovici* di-verged after cusp reduction had been initiat-ed, but before increase of number of prostate diverticula and speciation in the Ohrid basin began. The Biwa species, *G. biwaensis,* on the other hand, must have evolved from a different ancestral group within the genus. It is necessary to place it in a separate subge-nus, namely *Choanomphalodes,* a name erected by Lindholm (1927) as a subgenus of *Choanomphalus.*

It is strange that an endemic subgenus of *Gyraulus* has not evolved in Lake Baikal. *Gy-raulus* must have been present throughout Asia during the Tertiary (according to Zilch (1960: 110) since the Paleocene). This "gap" would not exist, however, if the following as-sumption proves true: evolution of an en-demic subgenus of *Gyraulus* may have taken place in the past but has continued until a still more aberrant group has been formed, namely *Choanomphalus* with its seven species endemic to Lake Baikal and one species endemic to Lake Khubsugul (=Ko-sogol). Indeed there are character states common to *Choanomphalus* and *Gyraulus* that can be regarded to be synapomorphous[2]
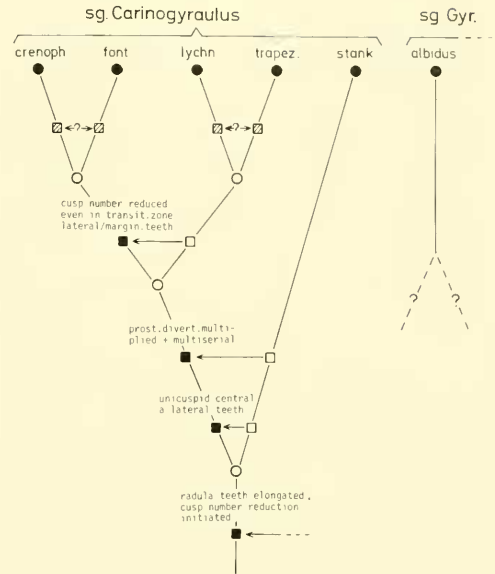
FIG. 106. Probable phylogenetic relationship in Macedonian *Gyraulus* species. Arrows are from plesiomorphous (open squares) to apomorphous characters (black squares). Shaded squares—di-rection of change uncertain. Open circles—hypo-thetical stem species. Black circles—contempo-rary species.

within the *Planorbis*-tribe. These are the gen-erally similar structure of the ♂ copulatory or-gan, including the hollow penial stylet formed by a rolled blade. Moreover, a lack of pallial folds in *Choanomphalus* (Hubendick, 1954: 504) relegates this species to the *Planorbis*-tribe. The genera of this tribe are united by the synapomorphy "loss of pallial folds." Characters giving *Choanomphalus* a unique state in the family are an additional gland complex opening immediately beside the ♂ genital pore, a greatly concentrated central nervous system, and the lack of a reflected ureter. None of these characters run counter to assuming its origin in the *Anisus-Gyraulus* group. Also Hubendick (1954: 508; 1955: 531–532) concluded that "the morphology of *Choanomphalus* seems to indicate that the genus is most closely related to *Anisus* and *Gyraulus* but has undergone a further evolu-tion." This view is shared by Kozhov (1963: 133) and Starobogatov (1958).

[2] We will call the characters or character conditions from which transformation started in a monophyletic group *plesio-morphous,* and the derived conditions *apomorphous.* . . . We will call the presence of plesiomorphous characters symple-siomorphy, the presence of apomorphous characters *synapomorphy,* always with the assumption that the compared characters belong to one and the same transformation series" (Hennig, 1966: 89).
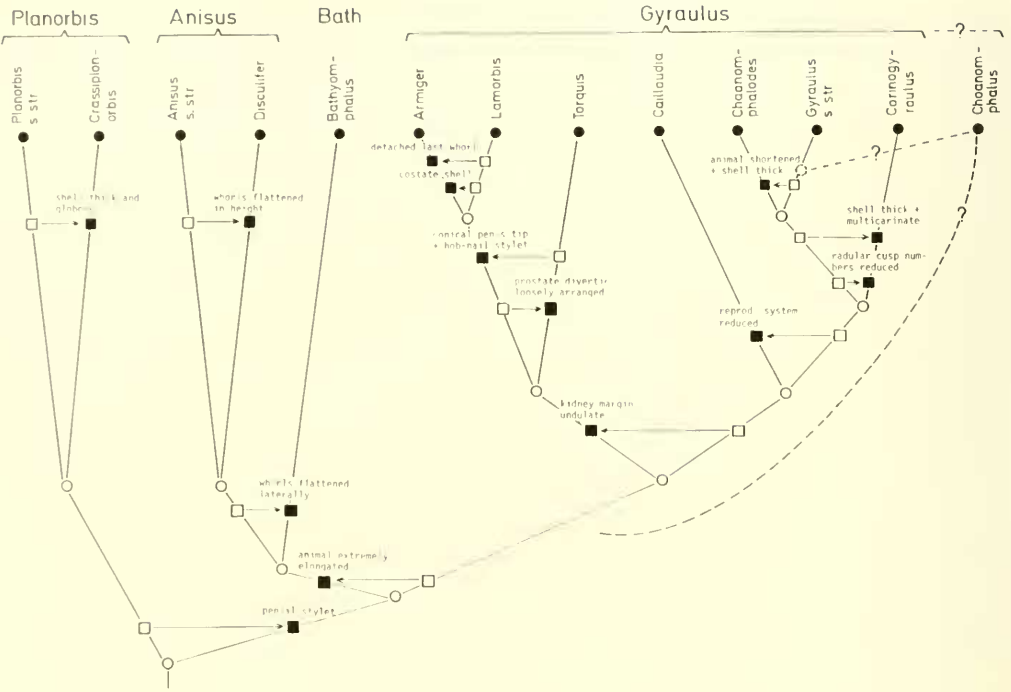
FIG. 107. The probable kinship relations in the *Planorbis*-tribe. For symbols see Fig. 106.

The question whether the *Choanomphalus* clade diverged before or after the parent species common to all recent *Gyraulus* species came into being, cannot yet be answered. If it diverged *after,* then it must show synapomorphies that are shared with a subgroup of *Gyraulus*. In this case *Choanomphalus* would have to be included in *Gyraulus* as a subgenus according to Hennig's (1966: 73) definition of monophyly: "A monophyletic group is a group of species descended from a single ("stem") species, and which includes all species descended from this stem species." Which group of *Gyraulus* species could have given rise to formation of a new clade in the Baikal basin? *Torquis* and *Lamorbis* occur in the Palaearctic but do not reach as far as Central Asia (Fig. 116). These two subgenera are sufficiently recognizable from shell characters that their past distribution in the Baikal region can be excluded as well. The only subgenera having reached Central Asia are *Armiger* and *Gyraulus* s. str. *Armiger* has too aberrant traits to be considered derived from a stem species shared with *Choanomphalus*. Thus only *Gyraulus* s. str. is left. This subgenus, however, is character-

ized exclusively by synapomorphies, thus forming a "remnant group" whose monophyletic status sensu Hennig cannot be proven. Should, one day, synapomorphous character states be found in *Gyraulus* species occurring, in past and present, in the Baikal region and should these synapomorphies be located in *Choanomphalus*, too, there would be no argument against including *Choanomphalus* in *Gyraulus* as a subgenus (Fig. 107, straight broken line). The genus *Gyraulus* would otherwise not keep its monophyletic status in Hennig's sense, as was also argued in the case of *Armiger*. If *Choanomphalus* branched off *before* the parent species of all recent *Gyraulus* species existed it must furthermore be regarded as a separate genus (Fig. 107, curved broken line), as all authors have done (Lindholm, 1927; Baker, 1945; Hubendick, 1954, 1955; Zilch, 1960).

Let us briefly consider the possibility that *Choanomphalus* branched off from a trunk that led to other genera of the tribe. *Planorbis, Anisus,* and *Bathyomphalus* presently extend to the Baikal region. The past existence of a species ancestral to—and only to—*Planorbis* and *Choanomphalus* giving

them the status of sister genera would mean: a structure as complex as the penial stylet in all genera of the tribe except *Planorbis,* would have developed twice independently. This is so unlikely that I can exclude it. *Anisus* and *Bathyomphalus* possess a derived character state not shared by *Choanomphalus*: an extreme elongation of the total body. In a branch leading to *Choanomphalus* this elongation would have had to revert to the shortened state. Such a reversion is not impossible, as *Gyraulus biwaensis* demonstrates. But it is improbable that all organs re-shorten to the same extent. The unusually long ♂ copulatory organ in *G. biwaensis* is an example of this partial re-shortening. In *Choanomphalus* there is no indication of a partial re-shortening (Hubendick, 1954). Consequently I should think it equally improbable to assume a common ancestor for *Choanomphalus* and *Anisus* or *Bathyomphalus* that is shared only by them (as a condition for finding sister groups).

The question of why there is no endemic subgroup of the genus in Lake Titicaca and Lake Tanganyika is, in the former case, easily answered: The Andes region has evidently been devoid of members of the genus *Gyraulus* at all times. From Lake Tanganyika a few records of "*Anisus*" or "*Gyraulus*" species are found in the literature. At least one such species was assigned to a different genus by Brown & Mandahl-Barth (1973), namely *Afrogyrorbis natalensis* (Krauss).[3] Lake Tanganyika was probably outside the geographical range of real *Anisus* or *Gyraulus* during most of its history. It is of interest, though, that a strongly carinate form, described as *Gyraulus bicarinatus* Mandahl-Barth (1954: 91) and somewhat ressembling ancient lake forms from other parts of the world, has been discovered in Lake Albert. However, *G. bicarinatus* belongs to *Afrogyrorbis,* too (Brown & Mandahl-Barth, 1973).

Finally the question of an affinity between ancient lake *Gyraulus* and fossil groups deserves attention. Shells from the Upper Miocene of Steinheim/Albuch, Württemberg, Germany, cover a wide range of forms from flat and almost planispiral to turreted and extremely pseudo-dextral. These fossil taxa have been placed in a single species, *Gyraulus trochiformis* (Stahl, 1824) (synonym: *Poecilospira multiformis* (Zieten, 1830)). Comparing shell characters of the Steinheim species

with those in the *Planorbis* tribe, particularly with thick-shelled and angled forms of ancient lakes, I do not object to grouping them in this tribe. However, the similarity of *P. multiformis* to *Gyraulus* is not greater than similarity to Paleocene *Carinulorbis* Yen, 1949. Even if we consider that *P. multiformis* may really have had anatomical characters in common with *Anisus* and *Gyraulus,* conchological differences between the Steinheim-group and any ancient lake *Gyraulus* would be greater than between distantly related standard *Gyraulus* species.

The probability substantiated above of an independent evolution of multicarinate and non-planispiral *Gyraulus* species in different parts of the world is one more reason not to overemphasize the possibility of a common evolution of Ohridan species and the Steinheim series, as was done by Polinski (1932) and accepted by Stankovič (1960: 244).

CLADISTIC ANALYSIS

Character Weighting

My study of morphological characteristics has revealed a number of qualitative or quantitative character states enabling me to distinguish species from each other. The use of such character states for characterizing and, thus, for identifying species, as discussed above, does, however, not necessarily mean that they are suited as tools in the analysis of genealogical relationship. One such character, to mention an example, is size. Within a certain range, enlargement or reduction of size appears to have happened independently in various groups where one observes giants or dwarfs. In a discussion on weighting of the "hob-nail-stylet" I shall show that isolated occurrences of dwarf-forms in the genus are encountered in Europe, Australia, Java, and Samoa. Of course, this does not preclude that splitting up of a tiny parent species may result in two sibling species maintaining their small size. Whether evolution took this course must be decided on two bases: (1) the occurrence of other derived characters common to these and only to these, and (2) a contact or overlapping of their geographical ranges at least in the past.

There are a number of processes besides convergent evolution that invalidate the re-

[3] *Afrogyrorbis* Starobogatov, 1967, described with the same type-species, *Planorbis natalensis* Krauss, has priority over *Ceratophallus* Brown & Mandahl-Barth, 1973.

sulting characters or lower the value of such characters for phylogenetic conclusions, although not for the discrimination of species. These are, among others, mosaic evolution, and gradual and sporadic reappearance of traits once lost during phylogeny.

Recognition of mosaic evolution (Mayr, 1975: 208) requires a great variety of characters undergoing transformation during evolution *after* the existence of the stem species of a taxon. In *Gyraulus* few characters of this kind have been observed, so that it cannot be judged whether or not mosaic evolution happened.

The problem arising through the second event mentioned above as limiting the value of a character may be elucidated by examining reticulate sculpture. Spiral striae, which in adult snails form this structure together with transverse striae (growth lines), are encountered in embryonic shells of all Planorbidae studied so far, as stated above. Since they occur in many other basommatophoran taxa, too, one may suspect that this sculpture once was common in adult shells of a taxon at the stem of the Basommatophora or one of their higher subordinate taxa. If this were the case (fossil records in support of this have not systematically been examined) then its complete absence in most planorbid shells including those of the closest relatives of *Gyraulus* must be secondary and its presence in several *Gyraulus* species either is due to reappearance of the ancestral structure or to a new acquisition. The observation that spiral striae on adult shells are an immediate continuation of embryonic striae supports the assumption of a reappearance. This would also facilitate an explanation of the obviously independent occurrence of spiral striae here and there (sg. *Lamorbis, Choanomphalodes, Gyraulus* s. str., *Carinogyraulus*), even in usually smooth-shelled groups, such as *G. chinensis spirillus*.

A new acquisition, however, can not be entirely excluded. The new striae could have started from the embryonic striae because the shell-forming mantle edge was functionally prepared for the formation of striae just at these sites. If my concept, established on several reliable characters (Fig. 107), is correct, new formations of striae, however, would have had to arise several times independently, since *Caillaudia, Torquis,* and *Armiger* always lack spiral striae.

The above speculation shows how difficult a decision is on what presence or absence of reticulate sculpture tells us about phylogenetic relationships. As long as there is no palaeontological evidence for spiral striation being ancestral, the problem must remain open. The value of the structure for cladistic analysis is, thus, zero. The suitability of a distinct reticulate sculpture for characterization and recognition of species, such as *Gyraulus albus* and *G. acronicus,* is not affected by this difficulty.

Characters particularly useful in the evaluation of relationship are all those that, besides a high stability, show (1) clear alternatives (example: undulate/straight kidney margins), (2) can be categorized as ancestral or derived with as little doubt as possible (example: pluricuspid/unicuspid radula teeth) and (3) tie in well with the geographical distribution of their bearers (example: the hob-nail-stylet in *Armiger* and *Lamorbis*).

Analytical Procedure

I have attempted to group species in supraspecific taxa according to a system expressing relationships and resulting in monophyletic groups. By relationship one means "overall similarity" as discussed by most authors (e.g. Hennig, 1966: 74). This can even be expressed in terms of mathematics and, consequently, meets the demand of modern biology for quantification, e.g. as in numerical taxonomy (Sokal & Sneath, 1963). Proceeding in this way one may establish a reasonable classification, but this does not necessarily yield groups united by relationship in a genealogical sense. Moreover, groups established in this way are "monophyletic" only in a sense that is not unequivocally defined. It was Hennig's (1950 and later) great contribution to recognize a logical and consequent way of phylogenetic research permitting clearcut and reproducible decisions. Of his many thoughts at least one has been generally accepted: the superiority of synapomorphous over symplesiomorphous characters in judging relationship, i.e. for the reconstruction of the actual course of the evolutionary process. Hennig's arguments in favour of this procedure are well known and need not be repeated here; they have not seriously been contradicted. Hennig's conception of monophyly (Hennig, 1950: 307 *et seq.*; 1966: 207; 1969: 17; 1974: 283), however, has not found general agreement. Inasmuch as the first thought in his definition is concerned, there is little controversy: "Only groups of species

that can ultimately be traced back to a common stem species can be called monophyletic" (Hennig, 1966: 207). Similar definitions have been in use a long time, with one minor, though important, difference. The generally accepted use of the term monophyly was sketched by Simpson (1961: 124): "Monophyly is the derivation of a taxon through one or more lineages . . . from one immediately ancestral taxon of the same or lower rank." Hennig defended his conception against this definition by pointing out that "the device of bisexual reproduction makes the species the real unit. New species can arise only through the breakdown of individually existing species" (Hennig, 1966: 207).

There has been much argument about the second part of Hennig's definition: ". . . it must be added that not only must a monophyletic group contain species derived from a common stem species, but it must also include *all* species derived from this stem species" (Hennig, 1966: 207). Acceptance of this postulate means that one has to break with familiar views about "natural groupings" as they appear to every unprejudiced observer. Reptilia, for example, cease to be a monophyletic taxon, whereas extremely dissimilar organisms, such as crocodiles and birds, are united in one taxon as Mayr (1975: 72–75) pointed out. Hence, the overwhelming majority of taxonomists disagreed with Hennig, i.e. all those who concentrated on the degree of divergence and not the stem group. Their sticking to a definition of monophyly excluding the demand for all species derived from the stem species being included was criticized by Hennig (1974: 283) with the simple, but irrefutible comment (translated): "Each pair of whatever species has a common ancestor. Following this criterion one may establish arbitrary grouping. It is only the postulate that animal species must have an ancestor common only to them in order to be members of a monophyletic group that makes definition clear and workable."

Actually, Hennig's conception has the advantage of being logical and allowing objective and reproducible conclusions and statements on phylogenetic relationships. It avoids decisions about the degree of overall similarity or dissimilarity which, in my opinion, must always be subjective because there will never be general agreement about which yardstick has to be used. Even mathematical methods will not be able to help in this respect, as drastic differences result depending on which

method of computation is employed using identical data (according to Mayr, 1975: 187).

The decision between (1) the logically consequent concept held by the "cladists" as Mayr calls them and based on a biological theory and (2) the "evolutionists'" conception of monophyly, taking into account the "dual nature of evolutionary change," but up to now based on no clear theory, is perhaps a matter of confession. For the analysis of relationship between taxa dealt with here I accept Hennig's principle and his definition of monophyly, although I acknowledge that there are some weaknesses in his works as, for example, the "deviation rule." Concerning the deviation rule Hennig himself (in Schlee, 1971: 28) more recently explained how his thoughts should be understood. He did not refuse Schlee's (1971: 27) remark, that this rule contributes to mastering a merely semantic problem.

Plesiomorphy and Apomorphy

"Recognition that species or species groups with common apomorphous characters form a monophyletic group rests on the assumption that these characters were taken over from a stem species that only they share in common, and which already possessed these characters prior to the first cleavage" (Hennig, 1966: 90). What criteria can be used to distinguish between plesiomorphous and apomorphous characters? (1) Apomorphous characters by definition appear later in geological time, i.e. in younger fossils, than plesiomorphous characters. (2) Plesiomorphous characters also occur in closely and distantly related taxa. Apomorphous characters are unique or rare and restricted to relatively small groups. (3) In groups with low vagility a character is probably apomorphous if it predominates in a restricted geographic area whereas taxa with the corresponding symplesiomorphous character have a wider distribution.

In the literature, a number of other criteria are offered, for example, in a paper dealing with relationships in advanced snakes (Marx & Rabb, 1972). In their work, the authors enumerate a total of 10 criteria for derivativeness. Several of them more or less repeat each other so that their number can be reduced. At least one of them, in my opinion, is open to circular reasoning, viz. "Correlation of derived states. A character state is derived if its occurrence is positively correlat-

TABLE 7. Characters in genera of the *Planorbis*-tribe. From left to right in columns: supposed direction of evolutionary change in characters within the tribe. +—regularly occurring; (+)—rarely occurring.

	1 Kidney margins		2 Mantle pigmentat.		3 Prost. div. number		4 Prost. div. arrangement		5 Vas deferens		6 Shape of penis sheath		
	straight	undulate	diffuse	patchy	high	low	closely spaced	loose	narrow	wide	cylindr.	club-shape	cylindr. again
Planorbis	+		+		+[1]		+		+		+		
Anisus	+	+	+		+[2]		+		+			+	
Bathyomphalus	+	+	+		+[3]		+		+			+	
Gyraulus	+	(+)	+	(+)	(+)	+	+	(+)	+	(+)		+	(+)
Choanomphalus	?			?		?		?	+[4]	?		?	(+)

	7 Penis tip thickening			8 Penis pore situated		9 Hollow penial stylet			10 Bursa copulatrix		11 Reticul. sculpt. (adult shell)	
	absent	present	reduced again	near tip	distant fr. tip	absent	present	"hobnail"	elong.	inflated	absent	present
Planorbis	+			+		+			+	(+)	+	
Anisus		+		+			+		+		+	
Bathyomphalus		+		+			+		+		+	+
Gyraulus			(+)	+[4]	(+)		+[4]	(+)	+	(+)	+	(+)
Choanomphalus		?					+[4]		+	?		(+)

[1] 19–57, Meier-Brook, 1976c.
[2] 13–80, Hudec, 1967.
[3] 26–43, Meier-Brook, unpubl.
[4] Hubendick, 1954.

ed with derived states of other characters. Such correlation of derived states of different characters probably results from common genetic history of taxa" (Marx & Rabb, 1972: 5). One should at least add ". . . correlated with *undoubted* derived states of other characters."

Of the three criteria mentioned above, the one based on fossil records does not help much in our case. The only characters preserved in the fossil state are those of the shell, and as shown in these studies, almost all reliable characters in this group are hidden in the animal.

Concerning the second criterion, i.e. the distribution of characters in *Gyraulus* and in other genera of the same tribe, I refer to Table 7. A character common to all of them is the lack of pallial folds. This synapomorphy does not appear in the table.

Most of the unique character states confined to small groups within the *Planorbis*-tribe occur solely in *Gyraulus* but these are not even in the majority of species. The following character states are regarded as apomorphous: undulate kidney margins, a patchy mantle pigmentation, a loose and irregular arrangement of prostate diverticula, an extremely wide vas deferens, the penis pore lying remote from the penis tip, an inflated bursa copulatrix. As to the number of prostate diverticula (Table 7, column 3), this is a quantitative character that may be subject to repeated reduction. Reduction or disappearance of an organ is therefore considered by many authors to greatly lower its value for phylogenetic analyses. But diverticula numbers in the *Planorbis*-tribe are not so unstable that extreme reduction would lack any significance for relationship. For example, the two African *Gyraulus* species, *G. costulatus* and *G. connollyi*, which are very similar in other characters, have extremely reduced diverticula numbers. It is very improbable that reduction took place independently after branching of their common stem species. Most probably their stem species already had reproductive organs greatly reduced in size and complexity and, among others, expressed in very low diverticula numbers.

The problem arising with an interpretation of shell surface structure (Table 7, column 11) has been discussed above. The completely smooth surface in postlarval shells of all genera of the tribe except in some subgroups of *Gyraulus* and *Choanomphalus* is striking. All other Recent planorbid genera have a smooth shell as well. Only few exceptions occur (e.g. *Bulinus reticulatus* Mandahl-Barth, 1954).

Since spiral striation incidentally appears or reappears in various species there is no clear decision in what direction transformation took place. Consequently the question has been left open (Fig. 112, shaded squares between *G. albus* and *G. piscinarum*).

In another case (Table 7, column 6) a rare character is seemingly shared by *Planorbis* and subgroups of *Gyraulus*. There is strong evidence that the *cylindrical penis sheath* in *G. riparius, G. rossmaessleri,* and moreover less regularly in *G. crista* and *G. malayensis* had their origin in the club-shaped penis sheath typical of *Gyraulus, Anisus,* and *Bathyomphalus*: in *G. crista* and *G. malayensis,* transitions between shapes are frequently found. On the other hand, the cylindrical shape of the penis sheath in *Planorbis* (Meier-Brook, 1976c, figs. 1, 6a), corresponds to the shape found throughout all other tribes of the family (Hubendick, 1955).

The form of the *penis tip* shows the same phenomenon (Table 7, column 7). A distal thickening of the penis in groups of the *Planorbis*-tribe as described above is unique in the family. Its lack in *Planorbis* is consistent with the state common to all other planorbid tribes. Within the genus *Gyraulus* intermediary stages are observed (Figs. 52, 63) between presence (Figs. 45, 72, 78, 81) and absence of the thickening (Figs. 55, 58, 60, 91). This suggests that its absence in certain *Gyraulus* species is secondary.

A *penial stylet* (Table 7, column 9) is absent in *Planorbis*. It is absent in the vast majority of Planorbidae though not in all of them. Its presence in various planorbid groups suggests that the question be examined whether stylets more probably have a common origin or have developed independently. A tendency to sclerotize the penis tip is observed in one or the other group, according to Hubendick (1955) in *Polypylyis* (*Segmentina*-tribe), *Planorbula* and *Promenetus* (*Helisoma*-tribe) as well as in *Physastra* (*Physastra*-tribe). Comparison of structure shows that all these stylets are solid and evenly transient from the penis tissue, both in form and in consistency. A picture of the penis tip of a *Physastra* species demonstrates this (Fig. 108). Stylets have also been reported from quite different groups, as in sacoglossan Opisthobranchia, where, according to Gascoigne (1974), there is a variety of stylets serving for transfer of sperm, either by conducting it to the bursa

FIG. 108.   Stylet in *Physastra* sp., L. Barracuta.

copulatrix or simply by hypodermic injection. None of these stylets has the exact characteristics of structure found in the four genera of the *Planorbis*-tribe listed in the table, i.e. the sharp delimitation against the penis tissue where it is, to a certain extent, movable like a door on a hinge. The broad base and the stylet itself consist of a rolled blade, leaving a tube inside and one proximal and one distal opening (Figs. 25 to 27). It is highly improbable that a stylet of such a complex construction has been formed more than once. Of all synapomorphies encountered in the tribe, the stylet is the one with the highest probability of being derived.

Probably two other genera with a sclerotized penis tip belong in the *Planorbis*-tribe: *Afrogyrus* Brown & Mandahl-Barth, 1973, and *Afrogyrorbis* Starobogatov, 1967. Pallial ridges are not mentioned; their lack would clearly place them here. The sclerotized tip of the penis in these two genera (Brown & Mandahl-Barth, 1973: fig. 4) is again so different that I conclude that it must have formed independently. An origin from a stem species that had the *Gyraulus* stylet is unthinkable. Let us assume that *Afrogyrus* and *Afrogy-*

rorbis belong in the *Planorbis*-tribe. Then they must have branched off somewhere between the stem species of the tribe (Fig. 107, basal circle) and the stem species of all *Planorbis* species.

The *hob-nail stylet* undoubtedly arose from the usual stylet by size reduction, associated with a narrowed penis sheath and penis, and a loss of the distal thickening of the latter. These reductions in size could be understood as a consequence of extreme size reduction of the whole animal as seen in the tiny species, *Gyraulus riparius* and *G. crista*. Accordingly, one might conclude that the origin of hob-nail stylets in these species took place independently, by convergent evolution, were there not a *Gyraulus* species with normal dimensions, i.e. *G. rossmaessleri*, which also has a hob-nail stylet. The fact that a species has these features although it could have maintained the normal penis, makes it likely that the following happened. Size reduction culminating in the evolution of *G. crista* and *G. riparius* took place independently (Fig. 111). So the hob-nail stylet came into being before such size reduction. Or, at least, hob-nail stylet formation was not an immediate consequence of an overall reduction in animal size.

Initially I hesitated to place *Gyraulus rossmaessleri* in the same subgenus as *G. riparius*. The reason was that conchologically *G. rossmaessleri* is so similar to *G. laevis* that paleontologists would find it difficult to tell them apart. On the other hand, there was the aberrant ♂ copulatory organ also shared by *G. riparius*. The undulate kidney also seemed to support the conchological decision. Later, when the undulate kidney was found to be present in *G. riparius* and *G. crista*, too, it became clear what had probably happened. The formation of prominent kidney septa took place when the parent species common to the subgenera *Torquis, Lamorbis,* and *Armiger* came into being. This parent species had the normal size of a *Gyraulus* and the normal rounded whorls. These shell characters are, therefore, symplesiomorphous to *G. rossmaessleri* and the subgenus *Torquis*, and are, thus, not suited to prove a close relationship between these. Moreover, abandonment of the closely and regularly arranged prostate diverticula, a process leading to the synapomorphy of the *Torquis* species, did not take place in *G. rossmaessleri*. Size reduction of the whole animal, including the shell plus flattening towards a peripheral angulation on the

other hand, is a process occurring repeatedly in species in different parts of the world, so that its independent occurrence in G. crista and G. riparius is not too unlikely. The different types of angulation (=formation of an edge) in the two species (Figs. 56 and 59) support independent formation of edges.

It would be of great interest to see how other species of the genus that have drastically reduced their size have managed the problems of housing the penis in the ♂ copulatory organ. There are tiny snails—evidently members of the genus Gyraulus—in different parts of the world, e.g. Planorbis singularis Mousson on Samoa (1.6 mm in diameter), Gyraulus terraesacrae Rensch in central Java (2.2 mm in diameter) and a species in Australia (2.5 mm in diameter). The only character common to these is their small size, so that independent reduction of size is highly probable. Do they possess a narrowed penis sheath and a conical penis tip with a hob-nail stylet?

Regarding the Australian species, here called G. sp. 1, I could examine specimens from two samples recently provided by Dr. B. J. Smith, of Melbourne. My prediction that size reduction does not necessarily cause formation of a conical penis tip and a hob-nail stylet, proved true. The distal part of the penis has a distinct though slight thickening with the penis pore near its middle and a "miniature edition" of a stylet in the normal form. The space problem in the actually narrow penis sheath has evidently been solved by stretching in length: the distal thickening is proportionally longer than usual in the genus.

The bursa copulatrix is of an elongate form in most Planorbidae. Inflated bursae are much rarer than in the Lymnaeidae, for example. There is a reasonable explanation for differences in abundance of the inflated bursa. The body whorl in lymnaeid snails leaves sufficient space for increased volume of organs, whereas in planorbid snails it is simply too narrow. When whorls are not so much flattened one can indeed find a more rounded bursa, e.g. in G. piscinarum (Fig. 71) and the more or less globose snails of ancient lakes (Fig. 96, 100, 103). On the other hand, as seen in G. ehrenbergi (Fig. 74) increase of whorl height does not automatically lead to inflation of the bursa. And an extreme inflation, as in G. eugyne (Fig. 94), certainly goes far beyond what is plausible as a simple consequence of whorl height increase. When an external or functional causative agent for an extreme morphological change is not obvious, the value of an otherwise apparently insignificant character is raised.

Two of the character states considered apomorphous on the strength of rarity within the Planorbis-tribe require some comment. These are the undulate kidney margins and the patchy mantle pigmentation. These characters force us to reconsider the problem of irreversibility. The question has already been discussed in connection with reticulate sculpture.

As shown above the undulate kidney margins are caused by distinct septa protruding into the lumen of the tubular kidney. According to Baker (1945: 12) in the Planorbidae the "central tube . . . is regularly marked by internal septa which project into the lumen for a greater or less distance." This would mean that the presence of septa is the rule in this family, and thus their absence rendering margins straight is the derived state. Baker's remark could imply that the formation of septa in subgroups of Gyraulus is merely a reversal of a loss, which, from time to time, occurred during evolution. Baker's figures of kidneys from a great variety of planorbid genera (Baker, 1945, pls. 44–47) do not show any sign of transverse septa except in a Gyraulus (G. circumstriatus (Tryon) (which is a Torquis species, where it has been placed by other authors on a conchological basis)) and two species of Helisoma. In the latter case I am not even sure whether it is not an artifact caused by fixation. I myself have never observed distinct septa in any living planorbid snail except in the case detected during the present studies. Should real septa be discovered in other planorbid groups these will probably prove to be non-homologous to those described here. The undulate kidney margins in some Gyraulus species are justifiably called apomorphous.

A probable reversal in evolutionary change is seen in the patchy pattern of mantle pigmentation. It is the rule in Planorbidae as well as in other basommatophoran families and also in various prosobranch groups. The patchy pigment is probably ancestral. Since a pigment pattern is not a complex structure only a small step is necessary from a distinct pattern to diffuse pigmentation and back again. Nevertheless this step has not occurred as frequently as one might suspect. Otherwise, the two alternate states should be distributed at random. In Lymnaeidae we

see two patterns. These are (1) a distinct pattern or (2) a more uniform pigmentation with small cutouts. These alternatives are usually clearly distributed and consistent within genera (genera have been generally retained by authors in spite of Hubendick's (1951) opinion), e.g. *Radix* and *Stagnicola,* respectively. The diffuse pigmentation of *Planorbis, Anisus, Bathyomphalus* and several *Gyraulus* species is at least so constant that it may be considered ancestral within the *Planorbis*-tribe. Accordingly the reappeared pattern is derived. This conclusion is supported by the geographic distribution of species with the patchy pigment pattern as it relates to the present systematic analysis of species. The patchy pigment pattern is missing in *Armiger, Lamorbis, Torquis, Choanomphalodes,* and *Carinogyraulus.* In the African subgenus *Caillaudia* the patchy pigment consists of a great number of unusually small spots, so that its independent derivation from diffuse pigmentation is not improbable. In the remaining species, tentatively united in a subgenus *Gyraulus* s. str. a patchy pigment pattern occurs only in N Europe, Asia and Indonesia. Of the two Australian species I have seen none[4] having mantle pigmentation at all, so that a decision is impossible. Whether the patchy pigment pattern occurs in the North American species is an important question that has not yet been examined. So far we may assume that reappearance of the patchy mantle pigmentation in *Gyraulus* has probably happened only once, in western Eurasia. From this point the first species with the patchy pattern spread and split up into a northern (*G. acronicus*) and a southern branch (the stem species of all species living in southwest, south, southeast and east Asia including Indonesia: *G. ehrenbergi, G. euphraticus* etc.) (Fig. 112). These two branches may have dispersed mainly in an easterly direction. While *G. acronicus* evidently did not evolve into isolated species, the southern stem species, on its way to the east, branched off several times. The latter process may have been favoured by the irregular shape of the continent south of the great mountain chain (Caucasus, Elburz, Hindukush, Himalaya). The many large peninsulas facilitated formation of peripheral iso-

lates, of which Mayr (1963: 513) says: ". . . most peripheral isolates do *not* evolve into new species, but *when* a new species evolves, it is almost invariably from a peripheral isolate." This is likely to be the case in S Asiatic *Gyraulus.* Secondary contact of peripheral isolates with the parental populations proved that reproductive isolation had not been completely achieved and thus we see the races of *G. chinensis.* In a few cases isolation was complete enough, and sibling species of *G. chinensis* (*G. euphraticus, G. tokyoensis*), or morphologically more dissimilar species evolved (*G. malayensis* and the diverse species of Sumatra and New Guinea) (Rensch, 1934; van Benthem-Jutting, 1963).

In summary, the more important apomorphous characters in the *Planorbis*-tribe may be categorized as follows: (1) Characters of high frequency in the tribe (but absence or rarity in other tribes of Planorbidae and related families), e.g. the hollow penial stylet; the thickened penis tip; the club shaped penis sheath. (2) Characters of low frequency in the tribe as well as in the family and order, or of low frequency in the tribe and scattered occurrence in the higher taxa indicating reversal of evolutionary change, e.g. the undulate kidney margins, loosely and irregularly arranged prostate diverticula, the penis pore being remote from the penis tip, the extremely widened vas deferens, the patchy mantle pigmentation. (3) Quantitative characters that lie beyond the usual range of variation, e.g. an extremely low or high number of prostate diverticula, an extremely inflated bursa copulatrix, a constant and distinct reticulate sculpture in the adult shell.

Characters listed under (1) serve to define relationships between the subgroups of the *Planorbis*-tribe. Characters listed under (2) mainly contribute to defining subgroups of the genus *Gyraulus,* whereas the characters of category (3) predominantly (though not exclusively) are autapomorphies[5] of species.

The nearly complete restriction of the category (3) characters to autapomorphies in this study is fortuitous. Each apomorphous feature, when appearing for the first time, is autapomorphous in one species (Hennig, 1966: 90). When it is stable enough, as required, this feature becomes the synapomorphy of

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[4] After completion of the manuscript I found the patchy pattern in *G. essingtonensis* (Smith) from the Kimberley region, West Australia (J. Walker legit 1979).

[5] An autapomorphy is a derived character state confined to one individual taxon. A synapomorphy is a derived character connecting two or more taxa.

all succeeding species. The extremely low-ered number of prostate diverticula in the two (or more?) species of the genus *Caillaudia* is one example. Even genera can be estab-lished from quantitative characters alone, as will be substantiated in the next chapter. In any case the point is: what is the probability of having the character *because* the common stem species had it? The probability should be high.

Cladograms

In his "scheme of argumentation of phylo-genetic systematics" Hennig (1966, fig. 22; 1969, fig. 2) establishes a phylogeny by working backwards from the synapomor-phous character states seen in recent taxa to the character states in stem taxa. The pro-cedure consists of three steps. (1) Collect in-formation on all characters that occur in more than one state in a group. (2) Decide what state is plesiomorphous and what is apomor-phous. (3) Arrange species (or higher taxa) so that every two or more species lie togeth-er if they share apomorphous character states (Hennig, 1966, fig. 22). A result of proceeding this way is a picture of the sequence of changes of character states ("transformation of characters" in Hennig, 1966). In the clado-grams (Figs. 106, 107, 111) squares indicate pairs of character states in the positions re-sulting from Hennigian arguments. White squares indicate the plesiomorphous state, black squares the apomorphous character state. All Recent species branching off one trunk carry the total number of character states (squares) indicated on the lines lead-ing to them in the cladograms. In some cases where the direction of character transforma-tion is not clear, squares are shaded. If two characters are uncorrelated, transformations of states are depicted by two pairs of squares, e.g. Fig. 106, transformation of plu-ricuspid to unicuspid radula teeth and of uni-serial to multiserial prostate diverticula. When two apomorphous character states are prob-ably linked, there is only one pair of squares, e.g. Fig. 107, transformation of thickened to conical penis tip and of the standard stylet to hob-nail stylet during evolution of the stem species of *Armiger* and *Lamorbis.*

It is evident that transformations of char-acter states could only have happened in a sequence as shown in Figs. 106, 107, 111. One exception is made, i.e. when multiple new character states appear in the same stem

species it is impossible to tell in what se-quence. But finding the sequence of trans-formation events between two branching points is irrelevant for relationship research.

The sequence of transformations deter-mined in a branch does not necessarily indi-cate absolute points of time that can be com-pared with those in a neighbouring branch. This can only be found in palaeontological studies. Hence the ordinate in Figs. 106, 107, 111, and 112 does not provide absolute mea-sures; it indicates only the relative sequence within each single branch.

Hennig's method of phylogenetic reason-ing does not involve measures of divergence or overall similarity. The positioning of taxa in a cladogram has no meaning as regards closeness of relationship. Each two branches originating from the same stem species can be exchanged, and the direction of arrows in the cladogram is accordingly random. In or-der not to express degrees of similarity, Re-cent taxa are shown at equal distances.

Subgroups in the *Planorbis* Tribe
and in the Genus *Gyraulus*

To determine if *Gyraulus* is monophyletic (sensu Hennig) one must study its closest rel-atives. The *Planorbis*-tribe is unquestionably a monophyletic taxon. The synapomorphies of its species are the lack of the three pallial ridges present in the other Planorbidae, short marginal radula teeth, and the presence of a separate prostate duct.

The hollow penial stylet is a distinct syn-apomorphy characterizing the majority of tribe members (Fig. 107). Other synapomorphies, not shown in the cladogram, due to lack of space, are the club-shaped penis sheath and the thickened penis tip. There is a limited number of species living in Europe and west Asia that share a character state belonging in the third category of apomorphies listed above i.e. extreme elongation of the body. This is not unique in the family. There are species similar in external appearance in South America, but remotely related to the *Planorbis*-tribe, namely *Drepanotrema* species. Besides some *Drepanotrema* species and those of *Anisus* and *Bathyomphalus* there are, as far as I know, no other planor-bid groups with an extremely elongated body.

Although convergent changes to an elon-gated body in species from South America and Eurasia is proved, there is no evidence of a selective value for this character state

FIG. 109. "Flatness indices" in *Gyraulus* (Gy) and related genera, *Anisus* (An = 2 × *vortex*, 1 × *spirorbis*, 2 × *leucostomus*) and *Bathyomphalus contortus* (Ba).

FIG. 110. Relations between whorl width and snail diameter in the stylet-bearing genera of the *Planorbis*-tribe.

that could explain the convergence. If elongation and slenderness had a selective value, convolution of such an animal would, in my opinion, invalidate any advantage. On the basis of similarity of relative body length I conclude that this transformation happened only once in the *Planorbis*-tribe. In the next clade one daughter species retained its roundish body cross section while the other became flattened laterally, yielding an unusually thick snail with a relatively low diameter, namely *Bathyomphalus* (Fig. 109, Ba). The daughter species with the plesiomorphous body form then divided once more resulting in the stem species of the two (three?) Recent species of the subgenus *Anisus* s. str. and that of the species *Anisus vortex* and *A. vorticulus* (sg. *Disculifer* C. Boettger). In the latter subgenus whorls are flattened as well but perpendicular to the direction seen in *Bathyomphalus*. Referring to the "flatness-index," all of the four (five?) *Anisus* species lie beyond the range of variation in *Gyraulus* (Fig. 109, An).

The width of the last whorl as a percentage of the total diameter is a good parameter to illustrate differences. Fig. 110 shows a broad gap between *Bathyomphalus* plus *An-*
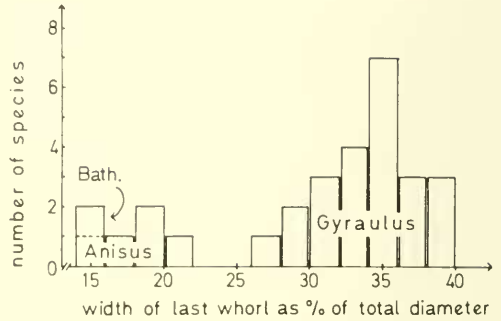
isus and *Gyraulus.* Class frequencies are distributed not only bimodally but also without contact or overlapping. The genus *Planorbis* is not inserted in the figure to avoid confusion. *Planorbis* lies well within the range of *Gyraulus* species with 27% (*Planorbis planorbis*), 28% (*P. intermixtus*) and 33% (*P. carinatus*).

I see no objection to conceiving the whole group of stylet-bearers as one genus, *Anisus,* as has been done by some authors. The group is clearly a monophyletic taxon. On the other hand, the gap (Fig. 110) separating *Gyraulus* and *Anisus/Bathyomphalus* justifies acceptance, at least of *Gyraulus,* as a separate genus (Mayr, 1969: 233). If *Gyraulus* has monophyletic status I prefer to leave it at the rank of a genus as most authors have done. A practical reason is the following. Indication of "*Gyraulus* sp." in publications provides much more information than "*Anisus* sp." or even "*Planorbis* sp."

Finding an apomorphy that is shared by all *Gyraulus* species but not by *Anisus* and *Bathyomphalus* would help to clearly state the monophyletic character of *Gyraulus.* Such an apomorphy would prove that *Anisus* and *Bathyomphalus* must have branched off the common trunk before the stem species of *Gyraulus* existed. One character state that should be synapomorphous to all *Gyraulus* species has not entered the cladogram (Fig. 107), because I am not sure enough about its reliability, but it should at least be considered. Two of the three *Planorbis* species have an angle or keel that is quite close to the upper side of the shell. This side is more or less plane, the whorls being flattened. The *Anisus* species have this flattened upper side as well;

moreover they have an angle or keel at exactly the same place as *Planorbis* (except *A. vorticulus* that is so extremely flattened that the angle appears to be in the middle). Thus the asymmetric shell seems to be plesiomorphous. Whenever a *Gyraulus* forms an angle or keel, this is situated symmetrically in the middle of the shell. Even in multicarinate species of old lakes, where additional angles or keels may appear near the under and upper side, their position is always different from that in *Planorbis* and *Anisus,* because the upper side is not plane, but marginally convex and centrally deeply concave (Figs. 99, 102). If one were able to accept this central angulation or carination or at least a tendency to form it as an apomorphy, there would be no question that *Gyraulus* is a monophyletic group in Hennig's sense, even when *Anisus* and *Bathyomphalus* are regarded as separate genera.

Summarizing the above discussions, according to the concept of so-called evolutionists (a higher taxon is an aggregate of related species separated from others by a discontinuity; Mayr, 1969: 88) there would be no doubt that *Gyraulus, Anisus* and *Bathyomphalus* are well separated genera. The strict monophyly concept of Hennig postulates synapomorphies uniting taxa to monophyletic higher taxa: "The possession of plesiomorphous characters (symplesiomorphy) does not justify the conclusion that the bearers of these characters form a monophyletic group" (Hennig, 1966: 90). The proof could perhaps be the central angulation or carination or a tendency towards this formation, if this can be accepted as a synapomorphy of *Gyraulus* species. If this character is not accepted as a synapomorphy (because there are *Gyraulus* groups constantly lacking an angled shell periphery), this would of course not be evidence against the monophyletic status of *Gyraulus.* A lack of synapomorphies merely means that proof of monophyly cannot be furnished.

Proceeding on the assumption that *Gyraulus* is in fact a monophyletic group, the further progress of evolution in most lines appears to be conclusive on the basis of synapomorphies discussed above (Fig. 107). Several of the probable evolutionary events have been presented in the remarks following descriptions of individual species. One problematic group, however, is left, i.e. the group of *Gyraulus* species placed in the provisional subgenus *Gyraulus* s. str. Again, the
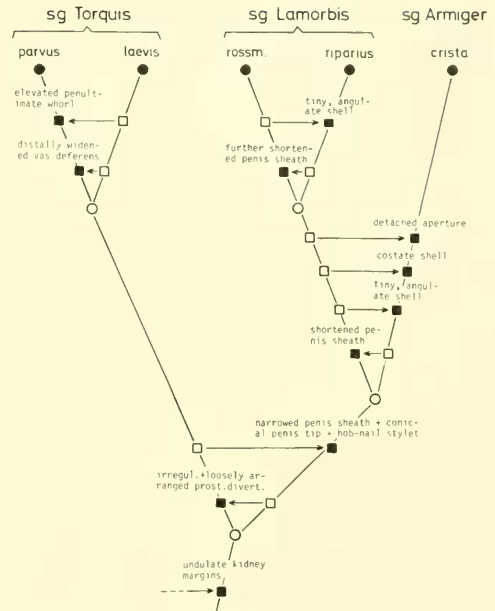

FIG. 111. The probable kinship relations in the *Gyraulus* species bearing undulate kidney margins.

monophyly of this group cannot be proved. Its pathway is marked by nothing but plesiomorphous character states. Following this pathway it is evident that in one lineage there is the group acquiring an undulate kidney (*Armiger, Lamorbis, Torquis*; Figs. 107, 111). After another branching a drastic reduction in volume and complexity of almost all reproductive organs occurred, i.e. in *Caillaudia.* The peculiar ancient lake species with distinct synapomorphies (*Carinogyraulus*) or an autapomorphy (*Choanomphalodes*) originated in two other such lineages. Consequently, the group called *Gyraulus* s. str. is a remnant group. The subgenus formation, shown in Fig. 107, namely *Carinogyraulus* and then *Choanomphalodes* and *Gyraulus,* could thus also have taken place in a different sequence. The sequence shown in Fig. 107 is, however, most likely from a geographical standpoint.

The ancestral stem species of Recent *Gyraulus* spread over wide parts of Laurasia after the stylet-bearing species diverged into two sister lineages, one producing elongated animals, the other keeping its normal body proportions (or perhaps producing the apomorphy of a central angle or keel). In the west part of Laurasia an organism evolved undu-

lating kidney margins, i.e. the stem species of Recent *Armiger, Lamorbis,* and *Torquis.* In the marginal southern zone of Laurasia a species branched off forming the stem species of *Caillaudia* with small and simple reproductive organs. In or near the present Ohrid basin a lineage appeared with thick-shelled and multicarinate snails reducing their radula cusps, i.e. the stem species of Recent *Carinogyraulus.* In Japan, finally, the stem species of *Choanomphalodes* branched off. What remained was *Gyraulus* s. str. retaining the plesiomorphous character states corresponding to the apomorphies mentioned above.

When Hennig's principle is applied the problem arises again and again that some species remain that carry only autapomorphies and are connected only by symplesiomorphies. "That a common stem form is shared by a group of species (a condition for a "monophyletic group" . . .) can be proved only by means of synapomorphous characters, not with symplesiomorphous characters" (Hennig, 1966: 90). *Gyraulus* s. str. therefore is considered here only a provisional subgenus. There is one reason why *Gyraulus* s. str. has probably to be considered even a "paraphyletic" group. The paraphyletic groups "have no ancestor in common only to them, and thus also no point of origin in time common only to them in the true historical course of phylogeny" (Hennig, 1966: 146–147). *Gyraulus* s. str. could be monophyletic (sensu Hennig) in two cases, namely (1) if *Carinogyraulus* and *Choanomphalodes* had a synapomorphy and, together, formed the sister group of the remaining *Gyraulus* species, or (2) if both *Carinogyraulus* and *Choanomphalodes* had split off from one and the same ancestor species. Concerning case (1), the derived character states in *Carinogyraulus* and *Choanomphalodes* turned out to have formed by convergence very probably. They are not sister groups. Concerning case (2), regarding the long distance from Europe to Japan it is probable that the species migrating eastward split into several lineages. The stem species of *Choanomphalodes* would then be not the same as the stem species of *Carinogyraulus.* These are the problems as regards the monophyletic status of a subgenus *Gyraulus* s. str. in a cladistic analysis according to Hennig. In contrast, the "evolutionists" and the numerical taxonomists accept paraphyletic groups (sensu Hennig) as monophyletic groups in

their sense. Basing their taxa on morphological similarity and separating their taxa on morphological divergence they would not face troubles in conferring monophyletic status to a subgenus *Gyraulus* s. str. as characterized in my study.

Within my provisional subgenus *Gyraulus* s. str. a monophyletic subgroup can be distinguished, namely the group of species with the synapomorphy "patchy mantle pigmentation" (Fig. 112, the seven species from the right). The two species carrying the plesiomorphous character state "diffuse mantle pigmentation," however, form the remnant group in this case, i.e. *G. albus* and the Near East species *G. piscinarum.* (A species with diffuse mantle pigmentation was, by the way, collected by Dr. H. Schütt in Turkey recently. It will have to be described as a new species showing that the remnant group consists of more than *G. albus* and *G. piscinarum.*) Should this group prove to be monophyletic it would have to bear the subgenus name *Gyraulus* s. str., whereas the group with the synapomorphy "patchy mantle pigmentation" would have to be in a new subgenus. For the time being, I prefer to wait for opportunities to examine more material from southwest, south and east Asia, hoping especially that samples from the Near East and North America will yield further insights. Only then will it be time to draw further conclusions about the remnant group. Finally the question must be asked: why not leave *Armiger* in genus rank? Mayr's (1974b) call that divergent evolution be considered in the reconstruction of dendrograms would favor a genus *Armiger.* Hennig replying to Mayr emphasized what he had explained in detail in previous works (among others Hennig, 1950: 308, and 1969: 17–20): "In reality there is a categorial difference between the monophyletic groups . . . ., possessing a stem species common *only to them,* and the non-monophyletic (paraphyletic and polyphyletic) groupings whose components also possess a stem species common to them but *not only to them*" (Hennig, 1974: 284, translated). Consequently raising *Armiger* to generic rank, although it has synapomorphous characters in common with the *Gyraulus* subgenera *Torquis* and *Lamorbis,* would mean that the genus *Gyraulus* would cease to be a monophyletic taxon in Hennig's sense. It would mean that *Gyraulus* in this case becomes a paraphyletic taxon. The distinction between paraphyletic and polyphyletic groupings, on the
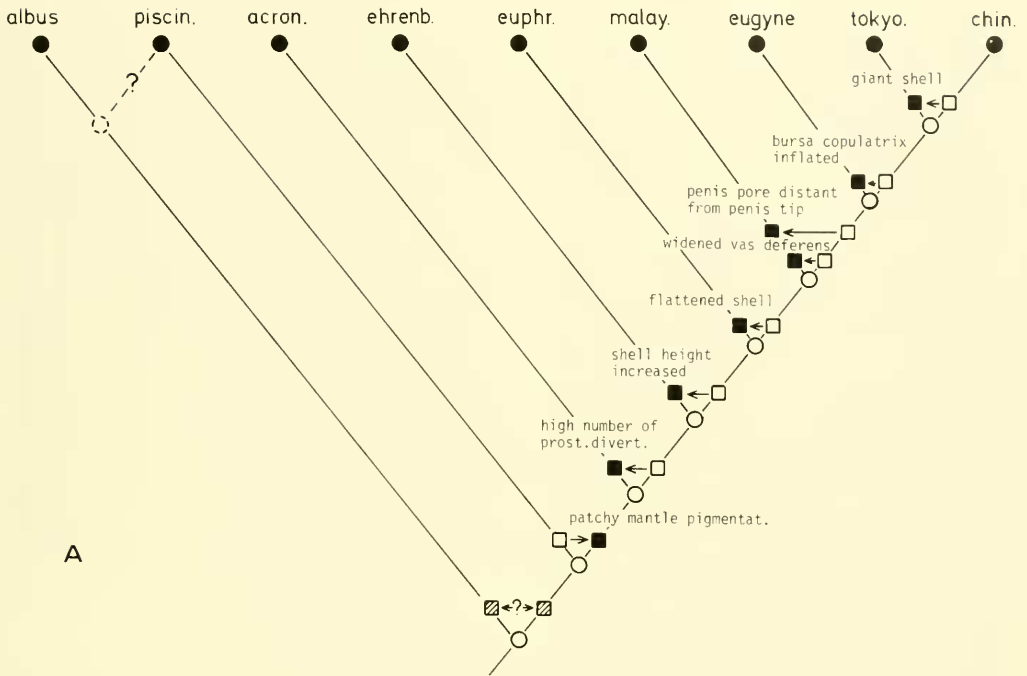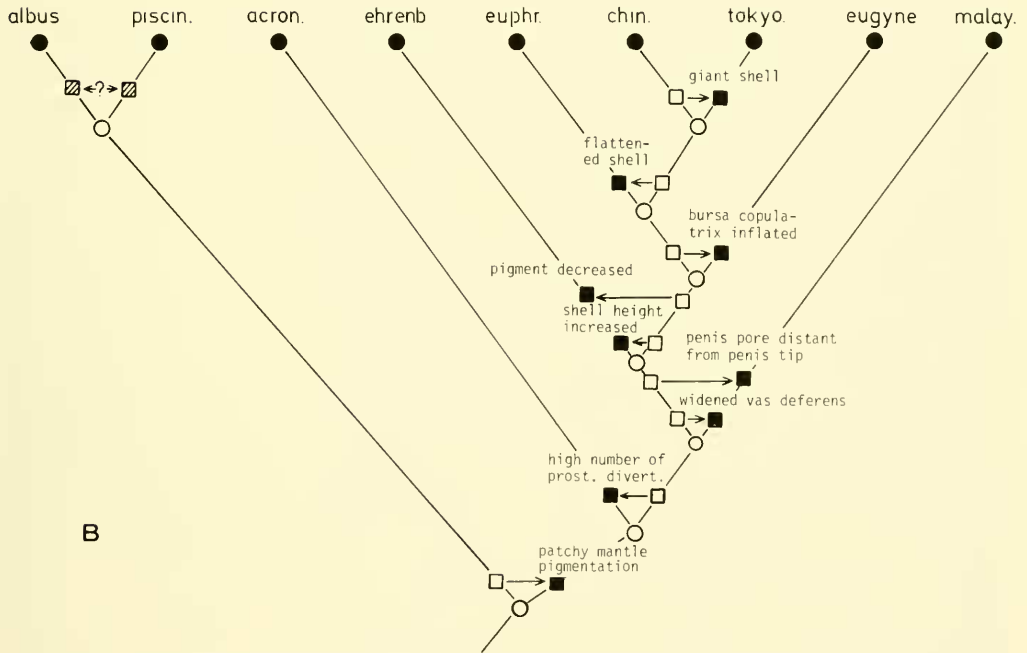
FIG. 112.   Two of the several possible kinship relations in the provisional subgenus *Gyraulus* s. str.

other hand, is only a methodological one and does not mean fundamental differences in genealogical relations, as has been demonstrated by Hennig (1969: 19; 1974: 284). As to the former genus name *Armiger*, there is no objection against its use as a subgenus. As illustrated in the dendrogram (Fig. 107) there is good reason to accept *Armiger* as the sister subgenus of *Lamorbis*.

Hennig (1966: 154) advanced the demand "that objects to which the same label is given must be comparable in some way" against the arbitrary treatment of ranking generally performed in the literature. Seeing the enormous difficulties in applying this principle to groups as different as annelids and mammals one will welcome his confinement to the demand that at least "sister groups must have the same rank" (Hennig, 1966: 159). This is reasonable and feasible. In practice, however, when interpreting Fig. 107, problems arise. The cladogram shows *Lamorbis* and *Armiger* as subgenera; they are sister groups. Together they form a group whose sister group is named *Torquis*. Thus *Torquis* does not rank at the same level as *Armiger*. It is desirable not to suppress the independence of the monophyletic group *Torquis* being expressed. Consequently *Torquis* could be raised to generic rank. Its sister group would be a genus "*Armiger* s.l." The two genera "*Armiger* s.l." and *Torquis* would perhaps present a group intermediate between a genus and a tribe. The sister group of this genus group would be the one comprising the groups named *Caillaudia* etc. through *Carinogyraulus*. In this group there would be a genus *Caillaudia*, whose sister genus would comprise the groups named *Choanomphalodes*, "*Gyraulus* s. str.," and *Carinogyraulus*. The next lower taxon not necessarily carrying a category name would be the group consisting of *Choanomphalodes* and "*Gyraulus* s. str." whose sister group is *Carinogyraulus*. If one sees a need for retaining the subgenera *Choanomphalodes* and "*Gyraulus* s. str.," *Carinogyraulus* could no longer stay at subgeneric rank because it does not hold the same level as e.g. *Choanomphalodes*. It would, strictly speaking, have a lower rank than generic and a higher one than subgeneric. This would, however, not contradict speaking of an unnamed category with a single subgenus, which has to carry the name *Carinogyraulus*. As ranking in one group is not dependent on how often branching occurred in its sister group, one must do what

has unexpressedly been done by systematists since long ago: (1) acknowledge a series of hierarchical intermediate categories (as many as branchings maximally occur), which may be named or unnamed; (2) in branches that have not split up as frequently as their sister branches insert an assumed additional "stem species" at the same level where in the sister group a branching point occurs. When doing so the difficulty seen above is easily solved: *Armiger* and *Lamorbis* are subgenera, together forming a taxon higher by one level, say "taxon of order Y." *Torquis* is a subgenus and that the only one of the sister "taxon of order Y." The three subgenera form a "taxon of order X," which, together with its sister "taxon of order X," forms the genus *Gyraulus*. Proceeding in this way, one avoids contradictions arising from strict consequences of applying Hennig's quite justified rule for equal ranking of sister groups. This is the procedure usual in handling monotypic taxa.

Absolute Age of Subgenera

The question as to how old the subgenera are arises because Hennig (1950: 255–261) had postulated that the absolute age of origin of a taxon should determine its rank. In the meantime manifold criticism apparently led him to abandon this concept or at least to mitigate it: ". . . phylogenetic systematics must be content with a much coarser time scale for its correlations" (Hennig, 1966: 183).

Determination of fossil snails should, of course, only be relied on when shells are characteristic enough to preclude errors. As confusion of many snail groups (*Planorbis*, *Afrogyrus*, *Promenetus*, and others) in Recent material demonstrates, a safe identification of *Gyraulus* in fossil samples seems to be impossible. This may explain fossil records of "*Gyraulus* s. str." from as early as the "Jurassic, ? Upper Cretaceous, Paleocene" (Zilch, 1960: 110). At least the two Mesozoic references are presumably erroneous. Subgenera that can more reliably be determined have been indicated from the Pleistocene (*Caillaudia*), Pliocene (*Carinogyraulus*), and Miocene (*Armiger*). Zilch (1960: 111) moreover records *Torquis* from the Miocene, but *Torquis* is often misidentified (confused with small *Planorbis*), even in Recent samples, as shown above.

Given current information on sea-floor-spreading (Scrutton, 1976; Thenius, 1977:

99), the disintegration of Laurasia into Palaearctic and Nearctic became complete in the Eocene. Accordingly, the ancestors of the European and American *Torquis* have lived in the Eocene at the latest. A migration, e.g. during the Pleistocene, via the Bering-bridge is highly improbable because there is no evidence that *Torquis* ever lived in Central and NE Asia.

As in the preceding case snails from other tribes are sometimes misidentified as *Planorbis*, because *Planorbis* has the plesiomorphous shell form that is shared by many other Planorbidae. According to Zilch (1960: 108) the oldest record for *Planorbis* is from the Upper Oligocene. Other close relatives of *Gyraulus* were recorded from Miocene (*Bathyomphalus*), Upper Miocene (subgenus *Anisus* s. str.) and Upper Pliocene (subgenus *Disculifer*). In view of the scattered nature of palaeontological data there is, at least for the time being, no chance of tracing the successive origin of taxa in geological time.

Speciation in *Gyraulus*

The probable course of speciation in the Ohrid basin group and in the group having the "undulate kidney margin" was previously discussed. The genus *Lamorbis* appears to consist of only two species, *Gyraulus rossmaessleri* and *G. riparius*. North America has many *Gyraulus* species not examined by me, but Baker (1945, pl. 15–19) figured the reproductive organs of most of them, and there is no evidence that any one of them has the features of the ♂ copulatory organ peculiar to *Lamorbis*.

The situation is apparently different in the subgenus *Torquis.* There is at least one more species in North America. Of the two sibling species, *Gyraulus parvus* and *G. laevis,* the North American one (*G. parvus*) has a wide distribution and a wide ecological range while the vicariant species in Europe (*G. laevis*) has a limited distribution and a narrow ecological range. A hypothetical explanation for such a difference could be the following. The common stem species of *G. parvus* and *G. laevis* was widely distributed in the now North American portion of Laurasia, where it was adapted to a wide range of habitats. A small peripheral section of the population split off and became reproductively isolated (either before or after complete separation of North America and Europe). This isolate spread over parts of Europe and invaded a limited num-

ber of habitat types, and that either (1) because of its restricted gene pool as compared with the large remaining population of their stem species or (2) because it found the majority of suitable ecological niches occupied already, perhaps by other *Gyraulus* species. Both factors may have contributed.

The phenomenon of pairs of vicariant subspecies or species strikingly different in distribution and environmental requirements is not rare. Hennig (1966: 59) quotes the situation in insects where cases are commonly encountered "in which, in addition to a common widely distributed euryoekous species, there is a second species that is very little different, less widely distributed and stenoekous." This is exactly the situation in the pair *Gyraulus parvus* and *G. laevis*.

Unlike the species of the subgenera *Torquis, Lamorbis* and *Armiger*, most species of *Gyraulus* s. str. lack distinct apomorphies. In this group at least two species have maintained the diffuse mantle pigmentation, *G. albus* (Europe, W Asia) and *G. piscinarum* (SW Asia). *G. albus* has distinct reticulate sculpture, *G. piscinarum* does not. It is not yet possible to decide which of these characters is more derived. All species of the Asiatic continent have patchy mantle pigmentation. I regard this to be their synapomorphy. Unfortunately all other apomorphies hitherto observed in the group are autapomorphies of species. The problematic situation for the phylogeneticist who deals with a group having only symplesiomorphies and species-autapomorphies can be well demonstrated with this group (Fig. 112). The sequence of evolutionary changes cannot be determined from morphology, and theoretically none of the n! (where n is the number of species with nothing but symplesiomorphies and autapomorphies) possibilities (5040 different sequences in our case, where n = 7) would have a higher probability than the other ones. My assumption is that a species most probably living in Europe or W Asia once developed patchy mantle pigmentation. This assumption increases the probability that the first splitting led to a northern branch, which did not split any more (at least not into reproductive isolates), i.e. *G. acronicus*, and a southern branch. We may thus assume that *G. acronicus* had its origin near the base of the tree of patchily pigmented species, as depicted in Fig. 112. The remaining six species could have arisen, theoretically, via 720 alternatives of

sequences, two of which are represented as Fig. 112A and B.

If my assumption is correct that the stem species of the southern branch spread to S Asia from W to E, two main alternative modes of further speciation are conceivable. (1) During dispersal in an easterly direction the southern branch split up several times leaving behind a series of species with limited distribution: *Gyraulus ehrenbergi, G. euphraticus. G. malayensis,* etc. (as shown in Fig. 112A, or something similar). This sequence would be consistent with the observation that "speciation apparently always goes parallel with a progression in space" (Hennig, 1966: 134). (2) Initially the southern branch spread into a vast area, as seen presently, and in the course of time peripheral isolates arose as has been shown for many animal groups, e.g. the tree snake *Dendrophis pictus,* the sandfly *Phlebotomus papatasii* (Hennig, 1966: figs. 16–17), and several groups of birds (Mayr, 1963: 496). It is unimportant whether the peripheral isolates are "only" subspecies or "already" reproductively isolated communities. If the stem species of all Asiatic *Gyraulus* at first spread from W to E Asia, we cannot even say whether an eastern isolate arose before a western, and the sequence may be completely random (Fig. 112B). At any rate it is obvious that the widespread species (the Rassenkreis or polytypic species *G. chinensis*) has maintained the most plesiomorphous characters and, thus, has diverged from its stem species to a lesser degree than the other S Asiatic species.

Reflexion about the first alternative, i.e. splitting of several species during easterly dispersal, brings us again to a discussion of the deviation rule. Hennig established it by stating: A species ceases to exist as a species when it breaks up into two species by partial ending of tokogenetic relations between its individuals" (Hennig, 1950: 102, translated). This rule has meantimes been heavily attacked by other taxonomists (among others Mayr, 1974b). In 1966, Hennig largely withdrew from this formulation, but he was still speaking of the "deviation rule, which is derived from the similarity distribution within species groups and which says when a species splits, one of the daughter species tends to deviate more strongly than the other from the common stem species (or from the common original condition)" (Hennig, 1966: 207). This is self-evident, and nobody has ever believed that two daughter

species would deviate to an exactly equal degree from their stem species! But Hennig sticks to a change of *both* daughter species in any case. There is one fact that makes it impossible to disprove Hennig's deviation rule. Our most objective species concept, the biospecies concept, can only be applied to contemporary organisms, not to organisms from different geological periods, as Hennig's disciple, Schlee, points out: "Concerning the species definition of the remaining population there is an uncertainty whether it is really identical—in a very strict sense—with the original population of the stem species. Species identity or unidentity, however, cannot be proved, because a biological species definition as a potential reproductive community is valid only for a point of time (temporal cross-section) and populations of successive times are, naturally, not open to crossing experiments" (Schlee, 1971: 28–29, translated).

The question whether a stem species can continue to exist, although new species have split off, is answered by Hennig as follows: "Stem species, from which two or more recent species have arisen (by whatever type of speciation), do not occur in the hierarchic system of recent species. They can be provided only by paleontology" (Hennig, 1966: 64). I do not concur because I consider *Gyraulus chinensis* as the continuously existing stem species of *G. ehrenbergi, G. euphraticus, G. malayensis,* etc. (Fig. 112). According to Hennig's deviation rule the stem species A of the S Asiatic *Gyraulus* species would have split at first into, let us say, *G. ehrenbergi* and a different new stem species A1. In a second cleavage the two species *G. euphraticus* and A2 would have appeared. Thus, in the five or more splitting processes the former stem species A would have changed five or more times. If unrestricted fertility between *Gyraulus* from Afghanistan and Korea should prove true, the existence of a biospecies *G. chinensis* would be clear. This would disprove the justification of Hennig's deviation rule, unless one assumes that the product of the latest splitting, A5 (or A6 or so) is the Recent species *G. chinensis. G. chinensis* then would have had to spread back from E Asia to W Asia covering the vast area now inhabited, which appears extremely improbable.

Would Hennig have voided the "rule" in our case? Probably not. Rather, he would warn us not to mix biological and genealogical systems (Hennig in Schlee, 1971: 28). In my

opinion, this is the point where dialectics begin.

Schlee apparently has a more realistic view of the situation at the species level such as in the Gyraulus group, saying "In monophyletic groups containing a taxon that is characterized by nothing but plesiomorphies, this taxon can be the stem species" (Schlee, 1971: 34, translated). This obviously applies to our G. chinensis and the group of its probable descendants. And this perhaps applies even to the relation between Gyraulus albus or G. piscinarum and the whole genus. (That G. albus has been designated type-species of the genus and is probably the species with the greatest similarity to the stem species of the genus, is, of course, a mere coincidence!)

Briefly returning to our alternatives of evolutionary processes in the S Asiatic region, one should see that there is fundamentally the same incompatibility of biological reality and the consequence of Hennig's deviation rule. A series of peripheral isolates would have to be graphically represented in the same way, for example like that in Fig. 112B. It would likewise raise the question: why should the stem species of the marginal new species have ceased to exist?

DISTRIBUTION AND CHOROLOGICAL ASPECTS

A combination of morphological and distributional features has long been used in phylogenetic arguments. The geographical implications in taxonomic research climax in the books of Rensch, particularly in his opus founding the "Rassenkreislehre" (1929). Our knowledge has recently been summarized in Hennig's (1966: 133) sentence: "Every species originally occupies a certain area, and the breaking up of a species into several reproductive communities usually, if not always, is closely related to the dispersal of the species in space." I will first discuss the distribution of Eurasiatic species of Gyraulus, as far as it is known, and of the species of the closely related genera.

The distribution maps (Fig. 113A–C) clearly indicate that the genera related to Gyraulus are restricted to the Palaearctic. The species of the genera Planorbis and Anisus primarily inhabit Europe; they only marginally extend into the central areas of Asia. The only species reaching as far as the Pacific coast

is Bathyomphalus contortus (Linnaeus). They all have in common a southern limit in the Mediterranean region, Turkey or the Black Sea, the Caucasus or Transcaucasia, the regions of the Caspian and Aral Seas and a line roughly crossing Kazakhstan and Mongolia. Fossil records remote from the Recent distribution areas have become known in Planorbis planorbis (Linnaeus), viz. from the Sudan and Ethiopia (Brown, 1965: 67). Planorbis species not mapped here are P. presbensis Sturany and P. macedonicus Sturany, both endemic to two Macedonian ancient lakes, and the group of P. atticus Bourguignat and P. intermixtus Mousson which live in the circummediterranean countries, eastward to Iran. They are probably not separate from each other (Meier-Brook, 1976c) but well isolated from P. planorbis, with which they share great parts of their geographical ranges.

As more or less all Planorbidae were once included in the genus "Planorbis" there was also a time when a great heterogeneous group of Planorbidae was named "Anisus." It might, therefore, appear as if I had not included the entire group of Anisus in the maps. Bollinger (1914) described an endemic species, Planorbis sarasinorum, from Lake Lindoe, Celebes, for example, which later usually was called "Anisus" sarasinorum. Its shell does not show any similarity with real Anisus species. The few whorls increase very rapidly, even more than usual for Gyraulus. Its aperture is trumpet-like. A sharp angle with a keel is situated in the middle of the periphery (material studied in ZMA). Moreover, Hubendick (1955) found a big gland in the preputium, which has not been found in any member of the Planorbis-tribe. Unfortunately I cannot discern from his semi-schematic figures the nature of the stylet. As has been shown above, formation of stylets has occurred independently in several groups of the family. It is highly improbable that "Planorbis" or "Anisus" sarasinorum is closely related to any Anisus species. Another question which cannot be answered is whether "Anisus" sarasinorum could have originated in the genus Gyraulus.

Another species recently referred to the genus Anisus is "A." pauxillus van Benthem-Jutting, 1963. This tiny snail from New Guinea, which its author classified in Anisus "only tentatively, because no soft parts are available," indeed has less rapidly increasing whorls than does Indonesian Gyraulus but still
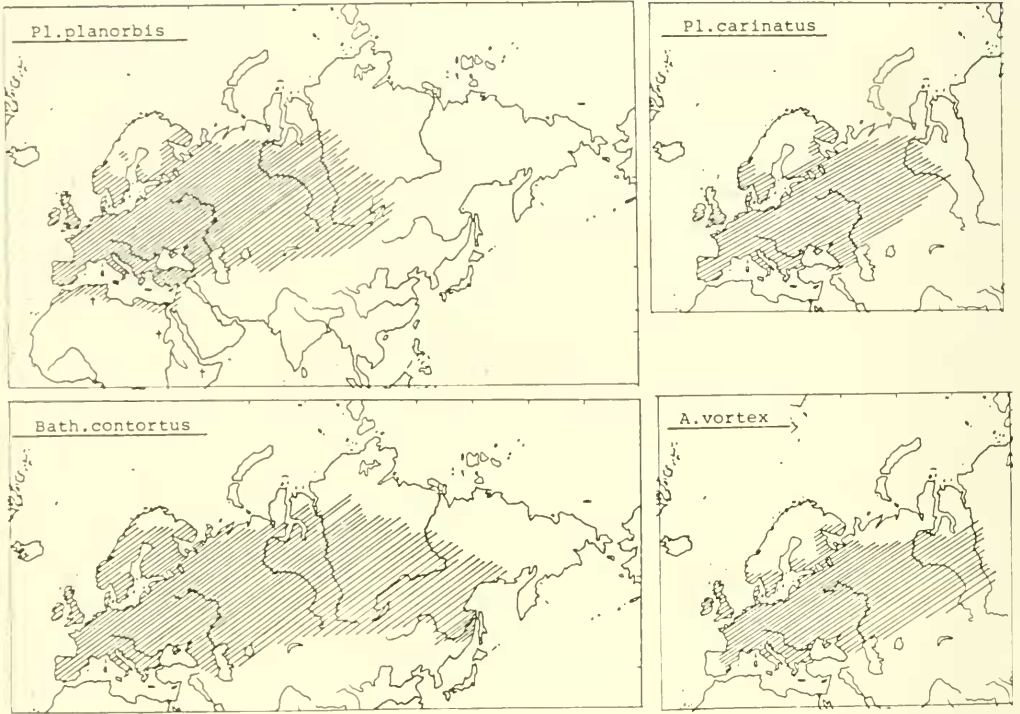
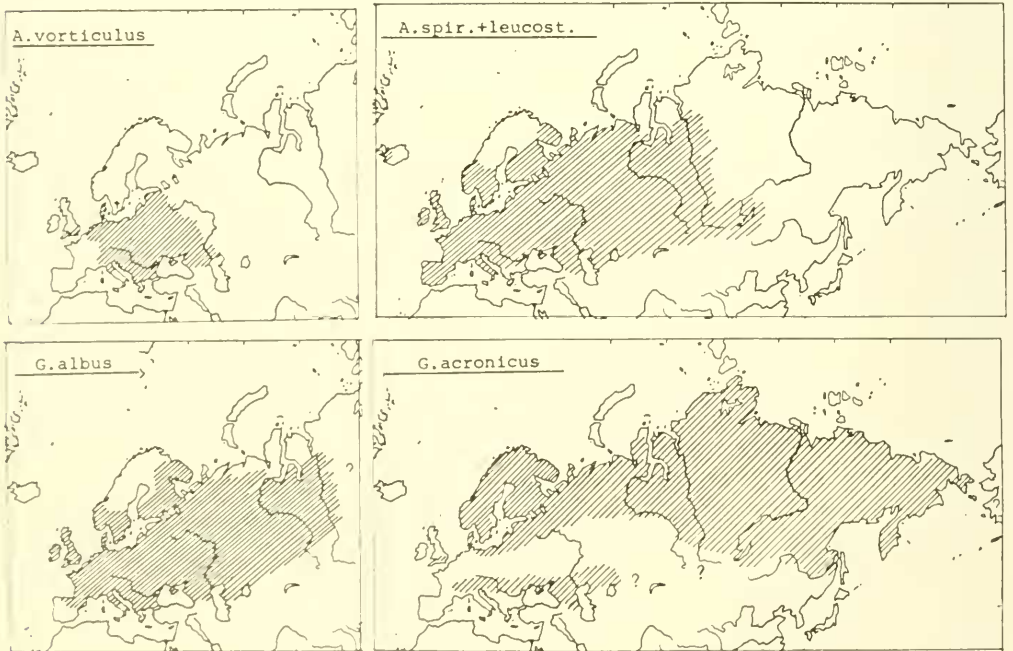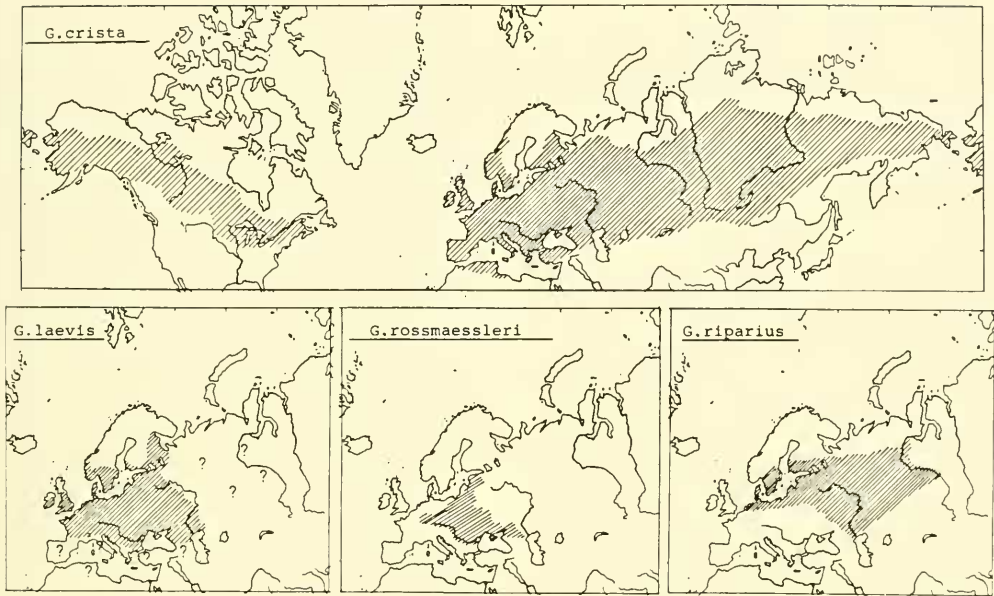FIG. 113A.   World distribution of *Planorbis*, *Anisus* and *Bathyomphalus*.

FIG. 113B.   World distribution of *Anisus* and Palaearctic *Gyraulus*.

FIG. 113C.   World distribution of Palaearctic *Gyraulus*.

decidedly more than in any of the European *Anisus* species. I expect that anatomical examination will reveal its close relationship with *Gyraulus* species. The nature of mantle pigmentation could supply the clue: if it shows a distinct pattern (besides other features of *Gyraulus*) it belongs in *Gyraulus*, because hitherto all *Gyraulus* snails seen from S and E Asia and the islands S of Asia have patchy mantle pigmentation. All four species of *Anisus*, on the other hand, lack this pattern. Some other snails listed as "*Anisus* species" by Baker (1945: 60) may either turn out to have only superficial resemblance with or to be merely synonyms of the European *Anisus* species. Presumably, the only other good species is *Anisus strauchianus* (Clessin). Being confined to S Russia, it fits within the distribution area of the genus. Fossil records, also of extinct species, do not lie beyond the Recent geographical limits of the genus.

We can thus state that all but one genus belonging to the *Planorbis*-tribe are restricted to the Palaearctic. The only genus that has spread to nearly every continent is *Gyraulus*. Should further studies reveal that the African genera *Afrogyrus* and *Afrogyrorbis* are also members of this tribe these would be further exceptions. North America, the Oriental, the Malay Archipelago, Australia, New Zealand and the Pacific Islands harbour *Gyraulus* only.

Of the *Gyraulus* species living in Europe only one has a Holarctic distribution: *G. crista*. The species with the second widest distribution is *G. acronicus*. It extends farthest to the N and displays a typical boreo-alpine disjunction, as is known for many organisms. Representatives of limnic animals with a similar distribution (accord. to Thienemann, 1950) are the water bug *Arctocorisa carinata* Sahlb., the chironomid midges *Paratrichocladius alpicola* Zett., *Pseudodiamesa nivosa* (Goethgh.), the copepod *Heterocope borealis* (S. Fischer), and several turbellarians. The boreal portion of the range of *G. acronicus* extends farther southward than that of the examples mentioned. It comprises the circum-Baltic countries as far as the Baltic terminal moraines reach. This area is shared by the cladoceran *Holopedium gibberum* Zadd., and two plant species typically associated with it: *Lobelia dortmanna* L. and *Isoetes lacustris* L. (Thienemann, 1950: 161). The only difference is that these three organisms exclusively inhabit lakes poor in lime, whereas *G. acronicus* requires a higher calcium concentration. Thienemann joins Ekman in applying the term glacial "pseudo-relics" to these species, previously often labelled "glacial relics." Since "glacial relics" should be restricted to species whose present distribution coincides with that during glaciation, Ek-

man introduced his term, defining it as follows (according to, and slightly modified, by Thienemann, 1950: 194, translated): "Pseudo-relics are faunal elements that are not relics in a certain area but have immigrated to it in the past when natural conditions, presently no longer existing, allowed access to the area." As to fresh-water molluscs this is true not only for *G. acronicus,* but also for some pill clams: *Pisidium lilljeborgii* Clessin, *P. conventus* Clessin, and probably also *P. hibernicum* Westerlund.

The two species of the subgenus *Lamorbis, Gyraulus rossmaessleri* and *G. riparius,* are not only stenoekous (or rather stenotopic, since the determining ecological factors are unknown) but also have a very limited distribution. *G. laevis* may be called central European. *G. crista* is apparently the only species of the *Planorbis*-tribe with a Holarctic distribution (Fig. 113C). There is, however, a strange difference in distributional character in the continents. *G. crista* is almost ubiquitous in the Palaearctic. In central Europe it is encountered in almost every water body (if not extremely soft); in constancy and abundance it is outdone at most by the lymnaeid snails *Radix peregra* and *R. ovata,* and perhaps also by *Anisus vortex.* In the Nearctic it is extremely scattered and rare. Clarke (1973: 406–409) surveying the fresh-water mollusc fauna of the Canadian Interior Basin found it in only two localities (of a total of 577 stations). He states that the species is "rare and local in distribution" in his investigation area "and probably in North America as a whole." He quotes La Rocque who lists 18 eastern North American localities from which this species has been recorded, but 15 of these are from Pleistocene sediments and only 3 represent living specimens. From this he concludes that "the relative abundance of *Armiger crista* in North America appears to have declined substantially since the Pleistocene." In eastern North America *G. crista* is particularly sporadic. It does not extend into the milder and warm climates, whereas the same species in the Old World inhabits circum-Mediterranean regions as far S as NW Africa. Its northern distribution, low abundance and low constancy in North America, together with its continuous distribution over N Asia, the Chukotskiy Peninsula, Alaska, and Canada strongly suggest that *G. crista* has reached the Nearctic continent via NE Asia. *G. crista* is certainly one of the fresh-water molluscs with the highest vagility. Its

extremely small size, its costae and spines and its quasi-omnipresence in water vegetation render it particularly suited for passive dispersal, e.g. by birds, to whose feathers it probably adheres easily. Since no older fossil records than from the Pleistocene seem to be known in North America (according to Clarke, 1973: 406) it may well be possible that the species was introduced to the North American continent after the connection (Bering-bridge) in the last glacial period in the Pleistocene had been formed that permitted considerable exchange of animals and plants (Thenius, 1977: 22). If this hypothesis is true, two (alternative or, more probably, joint) factors may determine the limited distribution and ecological range of *G. crista* in North America. (1) Only those individuals of the Palaearctic populations that were sufficiently adapted to a cold climate crossed the periglacial environment (tundra, steppe) of the Beringbridge. Hence this would mean a restricted gene pool of the American population, but not by chance (as responsible for the founder principle) but by selection. (2) Similarly, as hypothetically assumed for the European member of *Torquis* (*G. laevis*), the newcomer, *G. crista,* found most ecological niches occupied and could not settle as well as it might have done earlier.

The actual distribution of the SW, S and E Asiatic species is far too little known to present maps for them. I merely wish to demonstrate the relative uniformity of one taxonomically significant organ in the majority of samples (Fig. 114). I have omitted only those cases where several samples from neighbouring localities were checked, e.g. from Korea and Okinawa. All animals in these samples had the patchy mantle pigmentation indicating their evidently common origin. The majority of them have been included in *Gyraulus chinensis* in this study. Some marginal populations are considered separate species although the form of the penis sheath, penis tip, vas deferens and the position of the penis pore are virtually indistinguishable. These species, regarded as having originated as peripheral isolates (Fig. 115), are *G. euphraticus* (Fig. 116A; 115, 2), a species probably endemic to the Seychelles (nomenclature not as yet clear) (Fig. 114, D; Fig. 115, 3), *G. tokyoensis* (Fig. 115, 5; not drawn in Fig. 114, due to lack of space), *G. brongersmai* (Fig. 114, N; Fig. 115, 8); *G. tondanensis* (Fig. 116, Q; the penis was not recognizable, due to poor preservation, but the vas deferens and

the penis sheath suggest conformity with the species mentioned so far; Fig. 115, 7). *G. eugyne* (Fig. 115, 4) is probably also a peripheral isolate of the *G. chinensis*-Rassenkreis; but one should take into account that *G. acronicus* in this region probably almost reaches the range of *chinensis* (cf. Agócsi & Pintér, 1971); it could, thus, also be that *G. eugyne* is a peripheral isolate of *G. acronicus;* this should be examined in future studies.

The species examined from Mauritius under the name *G. mauritianus* shown to be identical with *G. chinensis* is obviously a recent introduction to the island through human activities. According to Starmühlner (personal communication) the fauna and flora of Mauritius is rich in anthropochorous elements from India. Brown (personal communication) claimed that Mauritius has in fact an endemic *Gyraulus* species, which has to carry the name *G. mauritianus* (Morelet) and which is said to be identical with the species of the Seychelles. I have not followed this question further; but in any case the *Gyraulus* inhabiting Mauritius and the Seychelles are distinctly different from any African *Gyraulus,* while anatomically it is very similar to the S Asiatic group. This suggests a close relationship that agrees with other biogeographic observations. Mani (1974: 645) lists a number of insect species endemic to the Seychelles but belonging in genera indigenous to India. Faunistic affinities to the Madagascan region are much smaller. According to Scrutton (1976) the Seychelles (unlike Mauritius) are most probably a fragment of the continental lithosphere that was left when India broke off and started to drift northward, about 60 to 70 millions of years ago. Up to that time, however, India was part of Gondwanaland and there would be no faunal relationship to taxa living in Laurasia. The present *Gyraulus* species of India certainly immigrated to the subcontinent only after India's fusion with the Asiatic continent. As long as Pangaea was intact, on the other hand, up to the Jurassic, *Gyraulus* certainly did not yet exist. The question concerning where the Seychelles received the stem species of their endemic *Gyraulus* species thus far remains unanswered.

The *Gyraulus* fauna of the Malay Archipelago deserves special attention. Since the pioneer work by Wallace this region has aroused biogeographers' interest. A sharp borderline, the Wallace line between faunal regions, runs between Bali and Lombok, between Borneo and the Celebes. West of it there are nearly exclusively Oriental elements with a very low proportion of Australian-Papuan elements; from Bali to Lombok there is an increase in Australian-Papuan elements and a decrease in Oriental elements. A less sharp line, Lydekker's line, between Australia/New Guinea and the Lesser Sunda Islands characterizes the eastern limit of Oriental elements, e.g. of the flying lizard *Draco lineatus* (Hennig, 1966: 136). Both lines coincide with the seacoast lines during periods of glaciation in the Pleistocene associated with a eustatic dropping of sea level. In between there are gradients in either direction. This region, named "indoaustralisches Zwischengebiet" by Rensch (1936: 251), is generally assigned the status of a different faunal region, the Wallacea (de Lattin, 1967: 273; Illies, 1971: 53). A line designating about equal portions of the respective faunal elements, Weber's line, is without interest here. It must be stated, however, that Wallacea has a number of genera and species of its own, including non-marine mollusks (Bollinger, 1914; Rensch, 1936).

While in Wallacea elements of Indo-Malayan and of Australian origin used to meet and overlap in many groups of organisms, Australia cannot be regarded as a source of *Planorbis*-tribe members. Consequently, spreading of *Gyraulus* in the Malayan Archipelago should have taken place mainly in easterly and southerly directions. The Australian *Gyraulus* fauna could have originated from only two continents: Asia and Africa. From South America, S of Venezuela, there are known neither Recent nor fossil *Gyraulus* species. One mode of extension of S Asian *Gyraulus* obviously was via Malacca to the Greater Sunda Islands. At present only four samples have been examined, one of which being *G. chinensis* from Malacca (Fig. 114, H), the remaining three belong to species with the aberrant characters in the δ copulatory organ, *G. malayensis* (Fig. 114, R, S, T). It is important to learn whether *G. chinensis* itself or a close relative with the corresponding plesiomorphous characters entered the Greater Sunda Islands and Bali at all. If not, the other *Gyraulus* species endemic to Sumatra (*G. proclivis* von Martens, *G. sumatranus* von Martens, *G. feuerborni* Rensch) and to Java (*G. terraesacrae* Rensch) probably share the striking features of *G. malayensis*. Spread of *G. malayensis* is likely to have ended at Wallace's line (distance be-
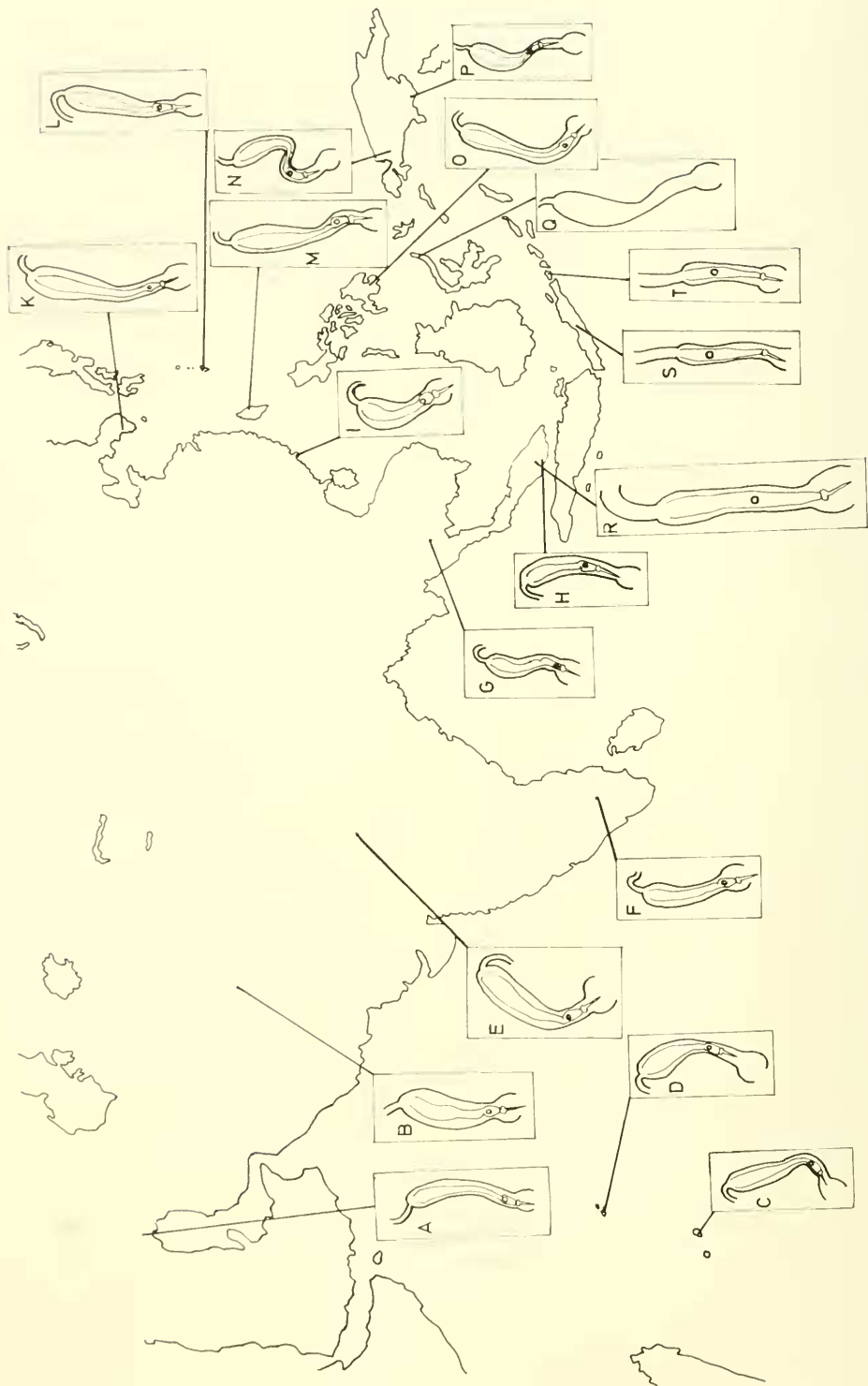
FIG. 115.   A tentative map of the approximate distribution of the southern branch of *Gyraulus* species with a patchy mantle pigmentation. White encircled area: *G. chinensis*. Shaded areas: peripheral isolates. 1 = *G. ehrenbergi*; 2 = *G. euphraticus*; 3 = a species endemic to the Seychelles; 4 = *G. eugyne* n. sp.; 5 = *G. tokyoensis*; 6 = *G. malayensis* n. sp. plus endemic spp. of Sumatra and Java; 7 = *G. tondanensis*; 8 = *G. brongersmai* plus endemic spp. of New Guinea.

tween Bali and Lombok scarcely 30 km, but depth of sea 300 m). Australia has evidently not received its *Gyraulus* fauna this way. The copulatory organ in the two Australian species studied is of the normal, i.e. plesio-morphous, form. The second route by which *Gyraulus* could have arrived at the Australian continent is the one via New Guinea. Firstly, *G. chinensis* itself has been encountered here (Fig. 114, P) (van Benthem-Jutting, 1963: 494), and secondly I note the similarity in essential anatomical features between (1) *G. chinensis,* (2) a species endemic to New Guinea, and (3) one of the Australian species examined. The New Guinean species in question is *G. brongersmai* van Benthem-Jutting (Fig. 115, N); the Australian species I wish to provisionally call *G.* sp. 2 (loc.: Bombala, New South Wales). These two share a

rather unusual shell form, recalling at first glance a *Segmentina* or *Hippeutis* in outline and even in surface character. I expect that study of more material will reveal that *G. brongersmai* and the Australian *G.* sp. 2 are sister species. Material of the other species described as endemic to New Guinea was not available for dissection.

How *Gyraulus chinensis* reached New Guinea from the Asian continent is a question not easily answered. *G. chinensis* is present in the Philippines (Fig. 114, O). *G. tondanensis* from North Celebes (Fig. 114, Q) has the general shape of the ♂ copulatory organ of *G. chinensis* as well. Moreover, Bollinger reported *Planorbis compressus* Hutton from the Celebes, which is probably a synonym of *G. chinensis*. Pleistocene land bridges between New Guinea and the Philip-

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FIG. 114.   Shapes of penis sheath and vas deferens and penis plus positions of penis pore in *Gyraulus* samples from S and E Asia. A—*G. euphraticus;* B, C, E through M, O, P—*G. chinensis;* D—*G.* sp., probably endemic to the Seychelles; N—*G. brongersmai* van Benthem-Jutting, 1963 (paratype); Q—*G. tondanensis* (Quoy & Gaimard, 1834); R, S, T—*G. malayensis* n. sp. Equal magnification in all figures. Localities: A—S Iran; B—Sayedabad; C—Mauritius; D—Seychelles; E—Bharatpur; F—Bangalore; G—Thailand; H—Malacca; I—Hong Kong; K—Kaejong; L—Motobu-cho; M—Taiwan; N—L. Tage, West Irian; O—Mindanao; P—Merauke, West Irian; Q—Tondano, Sulawesi; R—Kuala Lumpur; S—Bukateja, Java; T—Tasik Madu, Bali.
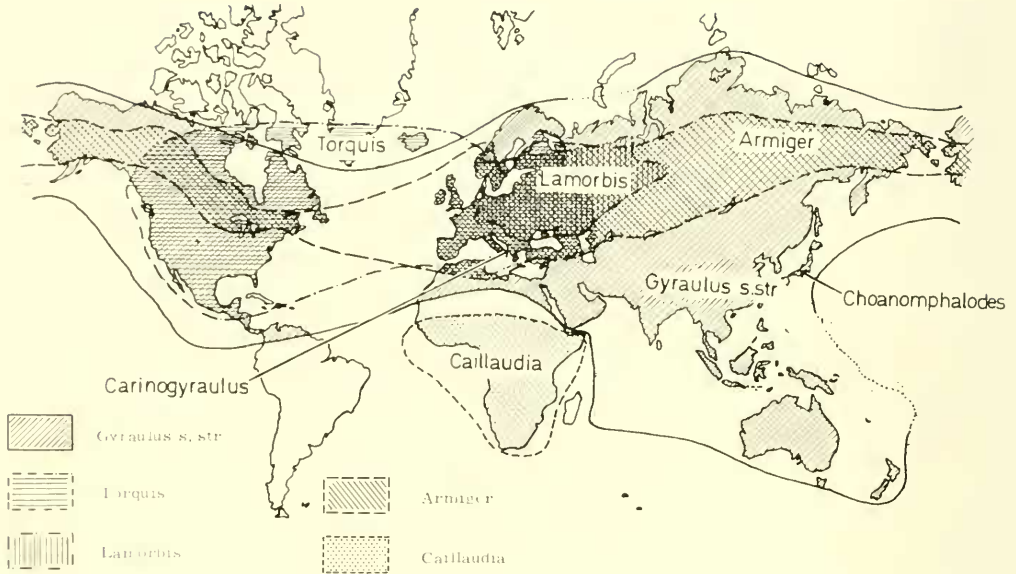
FIG. 116.   World distribution of *Gyraulus* subgenera.

pines cannot have existed considering the great depth of the sea between the islands. Moreover, the period since the Pleistocene seems to be rather short in view of the extensive speciation that has evidently taken place in New Guinea. Hence it follows that passive dispersal, probably by birds, remains the only explanation for the existence of *Gyraulus* in New Guinea.

Particularly close biogeographic relations between New Guinea and Australia on the one hand, and a very low affinity between the Australian fauna and that of the Greater Sunda Islands on the other have been well established in various groups of plants and animals (Keast, 1959; McMichael & Iredale, 1959: 241). My preliminary data presented so far as a by-product seem to be in line with these statements.

The second possible origin of Australian *Gyraulus* to be discussed is that from Africa. A prerequisite of this assumption would be (1) that transfer from Africa at least to the transantarctic continent happened before the Upper Jurassic/Lower Cretaceous, and (2) that snails were able to reach Gondwanaland from Laurasia despite their separation by the Tethys Sea. The probability of both is extremely low.

Surprisingly, however, I found a great reduction of portions of the reproductive system (e.g. two prostate diverticula!) recalling the apomorphous characters of the African species (subgenus *Caillaudia*) in one of the Australian species examined. It is the species, provisionally named *G.* sp. 1, from Benambra, E Victoria, mentioned above. Although shell characters are quite dissimilar, future students should pay particularly thorough attention to further similarities between this species and the African ones before the conclusion is drawn that similarities are merely a result of convergent evolution.

Finally, where were the centre of origin and the centre of differentiation? The following hypothesis is given. As the genera branching off near the base of the tribe (Fig. 107) are exclusively Palaearctic in distribution far beyond the present limits (except *Planorbis planorbis* in Africa), there can be no doubt that the stem species of all recent *Gyraulus* species lived in the Palaearctic region (Fig. 116). The stem species of the subgenera *Armiger*, *Lamorbis*, and *Torquis* split off, split once more, and the stem species of *Torquis* spread westward, joined by the plesiomorphous remnant group (with "straight kidney margins"), far beyond the limits of the present Palaearctic. In the Nearctic part of the then Laurasian continent speciation began, both in "*Gyraulus* s. str." and in *Torquis*. The European *Torquis* species, *G. laevis*, spread

in the counter-direction settling in the Palaearctic. *Lamorbis* remained limited to Europe; *Armiger* primarily inhabited the Palaearctic only and, if the above reflexions are correct, reached the Nearctic only during the Pleistocene.

A southern portion of the remnant plesiomorphous species, having reached Africa, was isolated by the formation of the Sahara desert. The remaining species having spread over the whole Palaearctic continent gave rise to a peculiar group in the Balkan region, and, independently, to that of another taxon in Japan. When, by the end of the Pleistocene, glaciations began, the stem species of *Carinogyraulus* and *Choanomphalodes* withdrew in the refugia of the Recent Lakes Ohrid/Prespa and Lake Biwa respectively.

The group that remained then split off a species developing the patchy mantle pigmentation. After another cleavage the two branches spread eastward separately, N and S of the great mountain chains. The southern branch cleft several times resulting in a greater number of peripherally isolated species.

A relatively basic (=early) diversification leading to the Recent subgenera took place in the European/West Asiatic region (3 subgenera, plus a subgenus in 2 Macedonian ancient lakes plus a subgenus probably immigrated from the Nearctic plus a marginal one in the south: *Caillaudia* (see Fig. 116)). Another, though minor, centre of differentiation can be located in the North American region (two subgenera plus one, probably more recent, immigrant). The large area of S and E Asia plus the Malayan Archipelago and Australia harbour species of only one subgenus, although extensive speciation (=differentiation) occurred.

We may, therefore, state that the centre of origin of the genus *Gyraulus* was probably the West Palaearctic. A primary centre of differentiation was in the same area, a secondary one in the Nearctic, and another one in the Indo-Malayan region.

Two of the main tasks of future research in taxonomy of the group will, consequently, be an elaboration of phylogenetic relations between the Palaearctic and the Nearctic taxa, and a study of speciation and dispersal in the Malayan Archipelago. Moreover, it is hoped that further knowledge of certain characters (especially the mantle pigmentation) in North American species will help to solve the question of a further division of the species group provisionally united in a "subgenus *Gyraulus* s. str."

DIAGNOSES OF SUBGENERA

1. Sg. *Gyraulus* s. str.

Type-species: *Planorbis hispidus*. Draparnaud 1805, designated by Dall (1870) (=*Planorbis albus* Müller, 1774).

The nominate subgenus, comprising the vast majority of *Gyraulus* species, differs from the other subgenera by the lack of characters typical for these other subgenera. The shell is always planispiral although the last whorl may descend towards the aperture. The aperture is more or less oval. The periphery is equally rounded, angled or keeled and may carry a periostracal fringe. The shell surface may be smooth, but in most species shows spiral striation, resulting in reticulate sculpture, usually visible at least on the upper side. The kidney has straight margins. The prostate diverticula, between 8 and 40 in number, are regularly and closely spread in a single row. The monophyletic status of this subgenus is uncertain because the character states common to all of its members are plesiomorphous ones. Of the Eurasiatic species examined the following are assigned to the nominate subgenus: *G. albus, G. acronicus, G. chinensis* with diverse races, *G. euphraticus, G. ehrenbergi, G. piscinarum, G. tokyoensis, G. eugyne* n. sp., *G. malayensis* n. sp.

2. Sg. *Torquis* Dall, 1905

Genus *Planorbis* subgenus *Gyraulus* section *Torquis* Dall, 1905: 83, 86.

Type-species: *Planorbis parvus* Say, by original designation.

Torquis differs from all other subgenera by the following characters: A planispiral shell with a nearly round aperture and the periphery neither angled, keeled nor fringed. The shell surface is always smooth, due to lack of spiral striation. The kidney is distinctly septate, thus appearing to have undulate margins. The prostate diverticula are arranged irregularly and usually scattered in a single row.

Eurasiatic species assigned here are: *G. laevis, G. parvus*.

3. Sg. *Lamorbis* Starobogatov, 1967

Genus *Choanomphalus* subgenus *Lamorbis* Starobogatov, 1967: 296.

Type-species: *Planorbis riparius* Westerlund, by original designation.

Lamorbis differs from all other subgenera by a cylindrical penis sheath which is, more-

over, distinctly shorter than the preputium, by a tapering penis tip with a hob-nail shaped stylet, a position of the penis pore relatively remote from the distal end of the penis, and a distinctly septate kidney as in *Torquis*. Species assigned here: *G. riparius, G. rossmaessleri.*

4. Sg. *Armiger* Hartmann, 1844

Genus *Armiger* Hartmann, 1844: 172, 219.
Type-species: *Nautilus crista* Linnaeus, by original designation.

Armiger differs from all other subgenera by its last whorl not embracing the penultimate whorl, but rather being ± loosely attached to the upper side of the latter, the peristome thus being continuous. *Armiger* has undulate kidney margins, a tapering penis tip with a hobnail shaped tiny stylet. There is probably only one species: *G. crista.*

5. Sg. *Carinogyraulus* Polinski, 1929

Genus *Gyraulus* subgenus *Carinogyraulus* Polinski, 1929: 161.
Type-species: *Gyraulus trapezoides* Polinski, by original designation.

Carinogyraulus differs from the other subgenera by a non-planispiral pseudodextral shell, a spire raised or flat, the left side carrying a funnel-like deep umbilicus delimited by an angle or keel. The whorls of the thickshelled species of the subgenus are sometimes reinforced by up to three keels. Central and lateral teeth of the radula are unicuspid, or cusp numbers at least partially reduced. Prostate diverticula are as in sg. *Gyraulus* s. str. or closely spaced in more than one row, totalling more than 40. The vas deferens is wider than in most species of the other subgenera.

Species assigned here are *G. stankovici* from Lake Prespa and *G. crenophilus, G. fontinalis, G. lychnidicus, G. trapezoides* from Lake Ohrid.

6. Sg. *Choanomphalodes* Lindholm, 1927

Genus *Choanomphalus* subgenus *Choanomphalodes* Lindholm, 1927: 182.
Type-species: *Choanomphalus japonicus* Preston (=*G. biwaensis*), by original designation.

Choanomphalodes differs from the other subgenera by a non-planispiral, pseudodextral shell, whose spire is flat to weakly raised. The periphery is tricarinate to rounded. The radula, vas deferens, and prostate are as in the sg. *Gyraulus* s. str., but the male copulatory organ differs from that in all other groups by its enormous length.

If *G. amplificatus* (Mori) should prove to be identical with *G. biwaensis,* the subgenus is monotypic.

7. Sg. *Caillaudia* Bourguignat, 1883

Genus *Caillaudia* Bourguignat, 1883: 99.
Type-species: *Caillaudia angulata* Bourg. (=*Planorbis costulatus* Krauss) by original designation.

The subgenus *Caillaudia* differs from all other subgenera by reproductive organs largely reduced in size and complexity: a tiny ovotestis, inconspicuous seminal vesicle, prostate diverticula reduced in length and number (3 to 12), irregular in shape and arrangement, the most distal one lying distinctly remote from the bursa copulatrix. Species assigned here: *G. costulatus, G. connollyi,* both in Africa south of the Sahara (Australian species?).

REDESCRIPTION OF *GYRAULUS*

The genus name was introduced in a publication by Charpentier (1837). He lists a subgenus "*Gyraulus* Ag. (Msc.)" of the genus *Planorbis* on p. 21 of his Catalogue des Mollusques terrestres et fluviatiles de la Suisse. A description or diagnosis is not added. The first species listed thereunder is *Planorbis hispidus* Drap.; as a synonym "*Pl. albus* Stud.*" is mentioned. *Pl. hispidus* Draparnaud, 1805, as the type-species was formally chosen by Dall in 1870.

The planorbid genus *Gyraulus* is conchologically and anatomically briefly defined by the following characters.

Shell—The shell is planispiral or, exceptionally (only in some ancient lakes), pseudodextral with elevated spire. The shell is small, 2 to 10 mm in maximum diameter. In planispiral species the mean height is $\frac{1}{5}$ to $\frac{1}{3}$ of the maximum diameter. The shell has 3 to 5 rapidly increasing whorls. The shell is deeply concave on the upper side, less concave or nearly flat on the under side. The aperture is roundish, ovoid or spindle-shaped at its outer margin. The surface is smooth to dull, with or without spiral striation. The color is light to dark corneous.

Animal—The animal is of a light to mod-

erate grey. The mantle pigmentation is diffuse to conspicuously patchy ("distinct pattern"). The kidney is long and narrow, with straight or undulate margins. The ureter is reflected. The pseudobranch is triangular to rectangular, with one longitudinal dorsal fold. The anus lies immediately to the right of this fold. The jaw is composed of a number of chitinized platelets. The radula formula is 12-1-12 to 27-1-27; the central teeth are biscuspid, with 3 additional denticles (2 lateral, 1 intermediate); the lateral teeth are tricuspid with usually 4 (2 lateral, 2 interstitial) additional denticles; the marginal teeth have up to 12 cusps formed by the 3 cusps of the lateral teeth and additional denticles which are increased in size and number. Cusp numbers are reduced (to one in central and lateral teeth) in forms endemic to Lake Ohrid basin, Macedonia. The alimentary tract has a more or less developed intestinal loop which is sometimes omitted. The ovotestis is composed of up to 40 lobes, which are arranged in 2 (rarely 3) rows. The proximal end of the spermoviduct is shorter than that distal to the seminal vesicle. The seminal vesicle has bulbous or spinous coils. The albumen gland is elongate triangular, convex dorsally, concave ventrally (the concavity harbouring the stomach). The female tract has no externally visible distinctions into oviduct, nidamental gland and uterus. The vagina is narrower, but often inflated close to the ♀ genital pore. The bursa copulatrix is narrow and cylindrical to inflated, the bursa duct being usually long and of varying width. The sperm duct is narrower than the oviduct. The prostate gland is separated from the sperm duct, with 3 to 40 diverticula emerging from the prostate duct. The diverticula are densely or loosely arranged in one row (exceptions with up to 70 or more diverticula, arranged in several rows, occur in species of the Lake Ohrid basin). The vas deferens usually narrows not far from the zone where the prostate duct branches off the sperm duct, then slightly widening, but still narrow towards the ♂ copulatory organ. In at least one species the vas deferens widens to approximately twice the diameter of the proximal half. In some species the vas deferens does not narrow, but is equally wide down to the ♂ copulatory organ; the ♂ copulatory organ is in shape well divided into a penis sheath and a preputium by a knob-like thickening. The penis sheath usually has a club-shaped proximal end, which is well set off against the vas deferens (exceptions in

forms of the Malay Archipelago, where it is scarcely wider than the unusually wide vas deferens). The penis sheath is more cylindrical and lacks a distinct club-like proximal thickening, but is nevertheless well distinguished from the vas deferens, in two European species (*G. riparius, G. rossmaessleri*). The distal end of the penis sheath is nearly closed by a muscular papilla of hemispherical shape. The preputium begins with a muscular ring called the diaphragm. The lumen of the preputium distal to the diaphragm is wide; towards the middle its lumen is usually narrowed by longitudinal, introverted folds which usually form pilasters; folds can be so weak that the preputial lumen appears nearly round. The penis sheath is usually of once to twice the length of the preputium (only in the two European species mentioned above distinctly shorter than the preputium). The penis is as long as the penis sheath, usually with a more or less conspicuous distal thickening (instead of the thickening there may be a conical tapering). The penis tip is equipped with a chitinized hollow stylet, which is clearly delimited against the penis tissue. The penis pore usually lies in varying portions of the thickened penis tip, exceptionally near the middle of the penis (forms of the Malay Archipelago, probably—according to Hubendick & Radoman, 1959—also in a species from Lake Ohrid).

SUMMARY

1. An approach is made towards basing the classification of the planorbid snail genus *Gyraulus* on as many characters as possible. The study is focussed on taxa inhabiting Europe and Asia with observations pertaining to other continents.

2. Shell proportions, as expressed by a "flatness-index" (introduced by Brown & van Eeden) and the ratio maximum shell diameter : whorl number are demonstrated in diagrams to show interspecific and infraspecific (both genotypical and ecophenotypical) variation. In one species, *G. albus,* shells of equal whorl numbers in lenitic biotopes are larger in diameter than in lotic biotopes (Fig. 6).

3. Influence of the usual fixing techniques on anatomical data is elaborated in one example. The length of the penis sheath is greatly affected by immersion of living *Gyraulus* snails in 70% ethanol, as compared with values for snails fixed after relaxation with

pentobarbital. The preputium does not appear to be significantly shortened.

4. Characters highly valued for species discrimination are among others: the distribution of pigment cells on the mantle to the right of the kidney; the presence or absence of distinct transverse septa in the tubular portion of the kidney rendering its margins "undulate" or "straight," respectively; the number of prostate diverticula, their shape and arrangement in the gland; the width of the vas deferens; the length ratio penis sheath : preputium; the shape of the penis tip and stylet, and the position of the penis pore. In certain groups peculiarities may occur in various other organs (radula, seminal vesicle, bursa copulatrix, bursa duct, etc.).

5. Europe outside Macedonia harbours five indigenous species. For their identification a key is presented which also permits recognition of two species recently introduced to Europe.

6. In Asia the number of species is much greater. N Asia is inhabited by *G. acronicus* (Fér.) only. A huge area of S Asia, from Iran to Japan and New Guinea, harbours forms so little different both conchologically and anatomically that they are probably not reproductively isolated and must, thus, be regarded as races of one polytypic species or "Rassenkreis": *G. chinensis* (Dunker) (synonyms: *G. convexiusculus* (Hutton), *G. spirillus* (Gould) and others). Species anatomically indistinguishable, but conchologically more or less distinctly different, are *G. tokyoensis* Mori and *G. euphraticus* (Mousson). They are considered separate species because they are said to be sympatric with *G. chinensis*, thus indicating reproductive isolation. There are some more species whose anatomical similarity suggests close relationship with *G. chinensis*; they are conchologically divergent species mostly endemic to island groups (Seychelles, Celebes, New Guinea). One species, on the other hand, conchologically so far indistinguishable, has quite aberrant anatomical features giving it a unique status. It is known from Malaya, Java and Bali and is described as a new species: *G. malayensis*. Another species named here is *G. eugyne* n. sp. from Inner Mongolia.

7. Abandonment of planispiral growth and formation of several angles or keels on the shell periphery in *Gyraulus* of ancient lakes is certainly due to convergent evolution. There is strong evidence that a species endemic to

Lake Biwa in Japan has a history different from that in a group endemic to the Macedonian Lakes Ohrid and Prespa.

8. For an analysis of phylogenetic relationships, Hennig's (1950 and later) recommendations are followed in a "search for the sister group" and a hierarchic system expressing the "recency of common ancestry" of taxa. Tools used in the analysis are common derived characters ("synapomorphies"). Moreover, Hennig's concept of monophyly is followed in this study.

9. Criteria for judging the apomorphous character states are discussed. Highly valued as being derived are characters of uniqueness or low abundance in the genus or in the family or higher taxa. Qualitative characters meeting these requirements are relatively rare in the genus, so that quantitative ones must be used in addition. In some cases, these are even used as synapomorphies of subgenera or genera, provided they display extreme values and appear to be sufficiently stable, e.g. the extreme elongation of the body in the genera *Anisus* and *Bathyomphalus*.

10. The systematic position of *Gyraulus* in the *Planorbis*-tribe is examined (Fig. 107). The species group bearing a hollow penial stylet (*Anisus, Bathyomphalus, Gyraulus*) is clearly a monophyletic group within the *Planorbis*-tribe. Since *Gyraulus* is likely to be a monophyletic group, too, maintenance of the three genera mentioned above is recommended because of clear gaps in their range of variation. *Anisus* and *Bathyomphalus* together form the sister group of *Gyraulus*.

11. Phylogenetic analysis in the genus *Gyraulus* reveals the existence of seven subgenera: *Torquis* Dall (Nearctic and W Palaearctic), *Lamorbis* Starobogatov (W Palaearctic), *Armiger* Hartmann (Holarctic), *Caillaudia* Bourguignat (Ethiopic), *Choanomphalodes* Lindholm (Lake Biwa, Japan), *Carinogyraulus* Polinski (Lakes Ohrid and Prespa, Macedonia), and a provisional "subgenus *Gyraulus* s. str." (cosmopolitan except South America and the Ethiopic region) (Figs. 107, 116). *Gyraulus* s. str. being a remnant group merely characterized by plesiomorphous character states is likely to be a paraphyletic group in Hennig's sense. Diagnoses of subgenera are given.

12. The impossibility of deriving sequences of evolutionary steps in groups sharing only in plesiomorphous characters is demonstrated in the remnant group, the provisional

"subgenus *Gyraulus* s. str." Sequences may, with a certain probability, be supposed from dispersal pathways only.

13. Incompatibility is shown between Hennig's "deviation rule" and biological reality in the case of peripheral isolates. The example advanced is the polytypic species ("Rassenkreis") *Gyraulus chinensis*, with marginal species such as *G. euphraticus, G. tokyoensis, G. malayensis* and others. *G. chinensis* is considered to be their "persisting stem species" although, according to this "rule," it ought to have changed its species status once at each time a peripheral isolate split off. A "persistent stem species of Recent species" is inconsistent with the deviation rule.

14. A limited geographical distribution and a narrow ecological range of the only *Torquis* species indigenous to Europe suggests that the subgenus primarily inhabited the western part of the former Laurasian continent and that *Gyraulus laevis,* the sister species of the Nearctic *G. parvus*, was split off from their common stem species as a small marginal portion of a large reproductive community. This is similar to phenomena encountered in insect groups where in pairs of vicariant species or subspecies one is often much less widely distributed and displays a much narrower ecological range than the other.

15. The centre of origin of the genus *Gyraulus* is probably the W Palaearctic, to which all its closely related genera are confined. With three subgenera of wider distribution plus one subgenus endemic to two ancient lakes in Macedonia plus one marginal subgenus in the Ethiopic plus one subgenus probably originating in the Nearctic, the W Palaearctic is at the same time regarded as the primary centre of differentiation. In the Nearctic there is a secondary one: two subgenera plus one subgenus probably acquired not before the Pleistocene. A third centre of differentiation, though only on the species level in a single subgenus, is the Indo-Malayan region (Fig. 116). Expansion probably took place radially from the W Palaearctic to the Nearctic, Africa, N Asia, and S Asia. Australia received its poor *Gyraulus* fauna evidently from Southeast Asia via New Guinea. An African offshoot in the Australian *Gyraulus* fauna, though unlikely, cannot yet be completely excluded.

16. A redescription of the genus *Gyraulus* Charpentier, 1837, is given using present knowledge on the variation of anatomical and conchological characters.

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LITERATURE CITED

AGÓCSI, P. & PINTÉR, L., 1971, Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. *Annales Historico-Naturales Musei Nationalis Hungarici, Pars Zoologica,* 63: 153–158.

AHO, J., 1978, Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. *Annales Zoologici Fennici,* 15: 146–154.

ALDER, J., 1838, Supplement to a catalogue of the land and freshwater testaceous Mollusca, found in the vicinity of Newcastle. *Transactions of the Natural History Society of Northumberland,* 1838: 337–342.

ALZONA, C., 1971, Malacofauna Italica. Catalogo e bibliografia dei Molluschi viventi, terrestri e d'acqua dolce. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 111: 1–433.

ANDERSON, T. W., 1958, *An Introduction to Multivariate Analysis.* New York, Wiley, 374 p.

ANNANDALE, N. & PRASHAD, B., 1919, The Mollusca of the inland waters of Baluchistan and of Seistan, with a note on the liver fluke of sheep in Seistan. *Records of the Indian Museum,* 18: 17–63.

ANNANDALE, N. & RAO, H. S., 1925, Materials for a revision of the Recent Indian Limnaeidae (Mollusca Pulmonata). *Records of the Indian Museum,* 27: 137–152.

AUERSWALD, B., 1851, in SCHMIDT, A., Malakologische Mitteilungen. *Zeitschrift für Malakozoologie,* 8: 179–192.

BAKER, F. C., 1928, *The fresh-water Mollusca of Wisconsin. Pt. 1. Gastropoda.* Wisconsin Academy of Science, Arts & Letters, xx + 507 p.

BAKER, F. C., 1945, *The molluscan family Planorbidae.* University of Illinois Press, Urbana, xxxvi + 530 p.

BECK, H. H., 1837, *Index Molluscorum praesentis aevi Musei Principis Augustissimi Christiani Frederici.* Fasc. I–II. *Mollusca Gastropoda Pulmonata,* 124 p.

BENTHEM-JUTTING, W. S. S. van, 1956, Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. V. Critical-revision of the Javanese fresh-water gastropods. *Treubia,* 23: 259–477.

BENTHEM-JUTTING, W. S. S. van, 1963, Non-marine Mollusca of West New Guinea. Part I. Mollusca from fresh and brackish water. *Nova Guinea, Zoology,* 20: 409–521, pl. 24–25.

BOLLINGER, G., 1914, Süsswasser-Mollusken von Celebes. *Revue Suisse de Zoologie,* 22: 557–579, pl. 18.

BONDESEN, P., 1950, A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. *Natura Jutlandica,* 3: 1–208.

BOURGUIGNAT, J. R., 1852, *Testacea novissima quae Cl. de Saulcy in itinere per orientem annis 1850 et 1851 collegit.* Lutetiae, 31 p.

BOURGUIGNAT, J. R., 1862, *Malacologie du Lac des Quatre-Cantons et de ses environs.* Paris, 72 p.

BOURGUIGNAT, J. R., 1883, Histoire malacologique de l'Abyssinie. *Annales des Sciences Naturelles, Zoologie,* 15: 47–162.

BRANDT, R. A. M., 1974, The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde,* 105: iv + 423 p.

BROWN, D. S., 1965, Freshwater Gastropod Mollusca from Ethiopia. *Bulletin of the British Museum (Natural History),* 12: 37–94.

BROWN, D. S. & EEDEN, J. A. van, 1969, The molluscan genus *Gyraulus* (Gastropoda: Planorbidae) in southern Africa. *Zoological Journal of the Linnean Society,* 48: 305–331.

BROWN, D. S. & MANDAHL-BARTH, G., 1973, Two new genera of Planorbidae from Africa and Madagascar. *Proceedings of the Malacological Society of London,* 40: 287–302.

BUCHNER, O., 1891, Beiträge zur Kenntnis des Baues der einheimischen Planorbiden. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg,* 47: 35–118.

BURCH, J. B., 1960, Chromosomes of *Gyraulus circumstriatus,* a freshwater snail. *Nature* (London), 186: 497–498.

BURCH, J. B., 1964, Cytological studies of Planorbidae (Gastropoda: Basommatophora). I. The African subgenus *Bulinus* s.s. *Malacologia,* 1: 387–400.

BURCH, J. B., 1967, Chromosomes of intermediate hosts of human bilharziasis. *Malacologia,* 5: 127–135.

BURCH, J. B. & NATARAJAN, R., 1965, Cytological studies of Taiwan freshwater pulmonate snails. *Bulletin of the Institute of Zoology, Academia Sinica,* 4: 11–17.

BURCH, J. B., WILLIAMS, J. E., HISHINUMA, Y. & NATARAJAN, R., 1964, Chromosomes of some Japanese Freshwater Snails (Basommatophora: Branchiopulmonata). *Professional Report 406th Medical Laboratory United States Army Medical Command, Japan,* p. 214–232.

CHARPENTIER, J. de, 1837, Catalogue des Mollusques terrestres et fluviatiles de la Suisse.

Denkschrift der Schweizer Gesellschaft für Naturwissenschaften, Neuchâtel, 1: 1–28.

CLARKE, A. H., 1973, The freshwater molluscs of the Canadian interior Basin. Malacologia, 13: 1–509.

DALL, W. H., 1870, On the genus Pompholyx and its allies, with a revision of the Limnaeidae of authors. Annals of the Lyceum of Natural History of New York, 9: 333–361.

DALL, W. H., 1905, Land and fresh-water mollusks of Alaska and adjoining regions. In: HARRIMAN Alaska Expedition Series, 13: 1–171, 2 pl.

DAVIS, G. M. & LINDSAY, G. K., 1967, Disc electrophoretic analysis of molluscan individuals and populations. Malacologia, 5: 311–334.

DAVIS, G. M. & YAMAGUCHI, S., 1969, The freshwater Gastropoda of Okinawa. Venus, 28: 137–152.

DOBZHANSKY, T., 1950, Mendelian populations and their evolution. American Naturalist, 84: 401–418.

DRAPARNAUD, J. P. R., 1805, Histoire naturelle des Mollusques terrestres et fluviatiles de la France. Paris, 116 p.

DUNKER, G., 1848, Diagnoses specierum novarum generis Planorbis collectionis Cumingianae. Proceedings of the Zoological Society of London, 16: 40–43.

EHRMANN, P., 1933, Weichtiere, Mollusca. In: BROHMER, P., EHRMANN, P. & ULMER, G., Die Tierwelt Mitteleuropas, 1: 1–264.

EICHLER, W., 1941, Korrelationen in der Stammesentwicklung von Wirten und Parasiten. Zeitschrift für Parasitenkunde, 12: 94.

FÉRUSSAC, J. B. L., 1807, Essai d'une méthode conchyliologique appliquée aux mollusques terrestres et fluviatiles. Paris, xvi + 142 p.

FRAGA DE AZEVEDO, J., MEDEIROS, L. D. DE, FARO, M. M. DA COSTA, XAVIER, M. DE LOURDES, GANDARA, A. F. & MORAIS, T., 1961, Os Moluscos de Água Doce do Ultramar Português. III. Molluscos do Moçambique. Lisboa (Junta de Investigações do Ultramar): 1–394.

GASCOIGNE, T., 1974, A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). Zoological Journal of the Linnean Society, 55: 53–59.

GERSTFELDT, G., 1859, Über Land- und Süßwassermollusken Sibiriens und des Amur-Gebietes. Mémoires des Savans étrangers (St. Pétersbourg), 9: 507–548.

GIUSTI, F., 1968, Notulae malacologicae.—IV. L'Isola di Montecristo e lo Scoglio d'Africa. Atti della Società Toscana di Scienze Naturali, B75: 239–254.

GOULD, A. A., 1859, Shells of the North Pacific Exploring Expedition. Proceedings of the Boston Society of Natural History, 7: 40–45.

GREDLER, V. M., 1859, Tirol's Land- und Süsswasser-Conchylien. II. Die Süsswasser-Conchylien. Verhandlungen der Zoologisch-Botanischen Gesellschaft Wien, 9: 213–308.

GROSSU, A. V., 1977, Le polymorphisme des gastéropodes et la possibilité d'identifier et de limiter l'espèce avec des méthodes biochimiques. Malacologia, 16: 15–19.

HADŽIŠČE, S., 1953, Prilog poznavanju Gastropoda Prespanskog i Ohridskog Jezera. Bioloski glasnik, II/B7: 174–177.

HAMILTON-ATTWELL, V. L. & EEDEN, J. A. VAN, 1971, A preliminary study on the microsculpture of the shell of some freshwater Basommatophora (Mollusca). Proceedings South African Electron Microscopy Society, Pretoria, 1971: 41–42.

HARTMANN, J. D. W., 1844, Erd- und Süsswassergastropoden der Schweiz. St. Gallen, 227 p.

HENNIG, W., 1950, Grundzüge einer Theorie der phylogenetischen Systematik. Berlin, Deutscher Zentralverlag, 370 p.

HENNIG, W., 1966, Phylogenetic systematics. University of Illinois Press, Urbana, Chicago, London, 263 p.

HENNIG, W., 1969, Die Stammesgeschichte der Insekten. Kramer, Frankfurt, 436 p.

HENNIG, W., 1974, Kristische Bemerkungen zur Frage: "Cladistic analysis or cladistic classification?" Zeitschrift für zoologische Systematik und Evolutionsforschung, 12: 279–294.

HESSE, P., 1928, Mazedonische Gastropoden, gesammelt von Herrn Prof. Dr. F. Doflein. Zoologische Jahrbücher; Abt. für Allgemeine Zoologie, 45: 1–30.

HUBENDICK, B., 1947, Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden. Zoologiska Bidrag från Uppsala, 24: 419–559.

HUBENDICK, B., 1949, Våra snäckor. Bonnier, Stockholm, 100 p.

HUBENDICK, B., 1951, Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature, and distribution. Kungliga Svenska Vetenskapsakademiens Handlingar, (4)3: 1–223, 5 pl.

HUBENDICK, B., 1952, On the evolution of the so-called thalassoid molluscs of Lake Tanganyika. Arkiv för Zoologi, (2)3: 319–323.

HUBENDICK, B., 1954, On the anatomy of Choanomphalus (Moll. Pulm.). Arkiv för Zoologi, (2)6: 503–509.

HUBENDICK, B., 1955, Phylogeny in the Planorbidae. Transactions of the Zoological Society of London, 28: 453–542.

HUBENDICK, B., 1958, The development of the penial stylet in Gyraulus (Moll. Pulm.). Arkiv för Zoologi, (2)11: 427–429.

HUBENDICK, B., 1960, The Ancylidae of Lake Ochrid and their bearing on intralacustrine speciation. Proceedings of the Zoological Society of London, 133: 497–529.

HUBENDICK, B., 1969, The Baikal limpets and their phylogenetic status. Archiv für Molluskenkunde, 99: 55–68.

HUBENDICK, B. & RADOMAN, P., 1959, Studies on the Gyraulus species of Lake Ochrid. Morphology. Arkiv för Zoologi, (2)12: 223–243.

HUDEC, V., 1967, Bemerkungen zur Anatomie von

Arten aus der Gattung *Anisus* Studer, 1820, aus slowakischen Populationen (Mollusca, Pulmonata). *Biològia (Bratislava)*, 22: 345–364.

HUTTON, T., 1849, Notices of some land and fresh water shells occurring in Afghanistan. *Journal of the Asiatic Society (Bengal)*, 18: 649–661.

ILLIES, J., 1971, *Einführung in die Tiergeographie*. Fischer, Uni-Taschenbücher, Stuttgart, 91 p.

INNES, W., 1884, Récensement des Planorbes et des Valvées de l'Egypte. *Bulletin de la Société Malacologique de France*, 1: 329–352.

JAECKEL, S. G. A., 1962, Ergänzungen und Berichtigungen zum rezenten und quartären Vorkommen der mittel-europäischen Mollusken. In BROHMER-EHRMANN-ULMER, *Die Tierwelt Mitteleuropas*. Quelle & Meyer, Leipzig, p. 27–294.

JAECKEL, S. G. A., 1967, Gastropoda. In ILLIES, J., *Limnofauna Europaea*. Fischer, Stuttgart, p. 89–104.

JOHNSON, R. I., 1964, The Recent Mollusca of August Addison Gould. *United States National Museum Bulletin*, 239: 1–182.

KEAST, A., 1959, The Australian environment. In KEAST, A., CROCKER, R. L. & CHRISTIAN, C. S., *Biogeography and ecology in Australia*. Junk, Den Haag, p. 15–35.

KEDDY, P. A., 1976, Lakes as islands: The distributional ecology of two aquatic plants, *Lemna minor* L. and *L. trisulca* L. *Ecology*, 57: 353–359.

KHAZANNIKOV, E. A., 1973, Mollusks of the genus *Gyraulus* (Gastropoda, Planorbidae) from the River Terek Basin. *Sbornik zoologićeskih' rabot (Ordzhonikidze)*, 1973: 129–137.

KLEMM, W., 1960, Mollusca. In STROUHAL, H., *Catalogus faunae Austriae*. Springer, Wien, VIIa, 1–VIIa 59.

KOZHOV, M., 1963, *Lake Baikal and its life*. Junk, The Hague, vii + 344 p.

KRAUSS, C. F., 1848, *Die Südafrikanischen Mollusken*. Ebner & Seubert, Stuttgart, 140 p.

KRULL, W. H., 1931, Importance of laboratory-raised snails in Helminthology with life history notes on *Gyraulus parvus*. *Occasional Papers of the Museum of Zoology, University of Michigan*, No. 226: 1–10.

KURODA, T., 1963, *A catalogue of the non-marine mollusks of Japan*. Malac. Soc. Japan, Tokyo, 71 p.

LASSEN, H. H., 1975, The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia*, 19: 1–8.

LATTIN, G. DE., 1967, *Grundriss der Zoogeographie*. Fischer, Stuttgart, 602 p.

LINDHOLM, W., 1927, Kritische Studien zur Molluskenfauna des Baikalsees. *Travaux de la Commission d'Etudes du Lac Baical*, 2: 139–189.

LINNAEUS, C., 1758, *Systema naturae. Regnum animale*, ed. 10, Lipsiae, 824 p.

LINNAEUS, C., 1767, *Systema naturae per regna tria naturae*, ed. 12. Holmiae, 532 p.

MacARTHUR, R. H. & WILSON, E. O., 1967, *The theory of island biogeography*. Univ. Press, Princeton, xi + 203 p.

MACHA, S., 1963, Neue Kenntnisse von der Weichtierfauna des Hultschiner Hügellandes. *Acta Musei Silesiae*, ser. A, 1963: 85–93.

MANDAHL-BARTH, G., 1954, The freshwater mollusks of Uganda and adjacent territories. *Annales du Musée Royal du Congo Belge Tervuren, Sciences Zoologiques*, 32: 1–206.

MANI, M. S., 1974, Biogeography of the peninsula. In: MANI, M. S., ed., *Ecology and biogeography in India*. Junk, The Hague, p. 614–647.

MARTENS, E. VON, 1867, Über die ostasiatischen Limnaeaceen. *Malakozoologische Blätter*, 14: 211–227.

MARX, H. & RABB, C. B., 1972, Phyletic analysis of fifty characters of advanced snakes. *Fieldiana Zoology*, 63: 1–319.

MAYR, E., 1963, *Animal species and evolution*. Harvard Univ. Press, Cambridge, Mass., xiv + 797 p.

MAYR, E., 1969, *Principles of systematic zoology*. McGraw-Hill, New York etc., xi + 428 p.

MAYR, E., 1974a, Difficulties and importance of the biological species concept. In MAYR, E., ed., *The species problem*. Arno Press, New York 371–388.

MAYR, E., 1974b, Cladistic analysis or cladistic classification? *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 12: 95–128.

MAYR, E., 1975, *Grundlagen der zoologischen Systematik*. Parey, Hamburg, Berlin, 370 p.

McMICHAEL, D. F. & IREDALE, T., 1959, The land and freshwater Mollusca of Australia. In KEAST, A., CROCKER, R. L. & CHRISTIAN, C. S., *Biogeography and ecology in Australia*. Junk, Den Haag, p. 224–245.

MEIER-BROOK, C., 1963, Über die Mollusken der Hochschwarzwald-und Hochvogesengewässer. *Archiv für Hydrobiologie Suppl.*, 28: 1–46.

MEIER-BROOK, C., 1964, *Gyraulus acronicus* und *G. rossmaessleri*, ein anatomischer Vergleich (Planorbidae). *Archiv für Molluskenkunde*, 93: 233–242.

MEIER-BROOK, C., 1976a, An improved relaxing technique for mollusks using pentobarbital. *Malacological Review*, 9: 115–117.

MEIER-BROOK, C., 1976b, The influence of varied relaxing and fixing conditions on anatomical characters in a *Planorbis* species. *Basteria*, 40: 101–106.

MEIER-BROOK, C., 1976c, The generic position of *Planorbis* (*Gyraulus*) *intermixtus* Mousson, 1874, and *Planorbis presbensis* Sturany, 1894 (Gastropoda, Basommatophora). *Basteria*, 40: 107–118.

MEIER-BROOK, C., 1978, Calcium uptake by *Marisa cornuarietis* (Gastropoda; Ampullariidae), a predator of schistosome bearing snails. *Archiv für Hydrobiologie*, 82: 449–464.

MILLER, B. B., 1966, Five Illinoian molluscan faunas from the southern Great Plains. *Malacologia*, 4: 173–260.

MOITESSIER, P.-A., 1867, Histoire malacologique du département de l'Hérault. *Revue et Magazin de Zoologie*, sér. 2, 19: 421–445.

MORI, S., 1938, Classification of the Japanese Planorbidae. *Memoirs of the College of Science, Kyoto Imperial University*, ser. B, 14: 279–300.

MOUSSON, M. A., 1874, Coquilles terrestres et fluviatiles recueillies par M. le Dr. Alex. Schlaefli dans l'Orient. *Journal de Conchyliologie*, 22: 5–60.

MÜLLER, O. F., 1774, Vermium terrestrium et fluviatilium seu animalium infusorium helminthicorum et testaceorum non marinorum succincta historia. Heineck & Faber, off. Mölleriana, Hauniae et Lipsiae 2: xxxvi + 214 p.

NATARAJAN, R., BURCH, J. B. & GISMANN, A., 1965, Cytological studies of Planorbidae (Gastropoda: Basommatophora). II. Some African Planorbinae, Planorbininae and Bulininae. *Malacologia*, 2: 239–251.

ODHNER, N. H., 1929, Die Molluskenfauna des Tåkern. *Sjön Tåkerns. Fauna och Flora*, 8: 1–129.

ODHNER, N. H., 1956, Distinctions between *Anisus* (*Armiger*) *crista* (L.) and *Anisus* (*Gyraulus*) *riparius* (West.). *Proceedings of the Malacological Society of London*, 32: 127–131.

PACE, G. L., 1973, The freshwater snails of Taiwan (Formosa). *Malacological Review Suppl.*, 1: 1–118.

PAN AMERICAN HEALTH ORGANIZATION, 1968, A guide for the identification of the snail intermediate hosts of schistosomiasis in the Americas. *Pan American Health Organization, Scientific Publication*, 168: ix + 122 p.

PARAENSE, W. L., 1966, "*Biomphalaria amazonica*" and "*B. cousini*," two new species of neotropical planorbid molluscs. *Revista Brasileira de Biologia*, 26: 115–126.

PATTERSON, C. M., 1971, A karyotype technique using freshwater snail embryos. *Malacological Review*, 4: 27.

POLINSKI, W., 1929, Die reliktäre Gastropodenfauna des Ochrida-Sees. *Glas Srpske Kraljevske Akademije*, 173: 131–178.

POLINSKI, W., 1932, Die reliktare Gastropodenfauna des Ochrida-Sees. *Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere*, 62: 611–666.

PRESTON, H. B., 1916, Descriptions of new freshwater shells from Japan. *The Annals and Magazine of Natural History*, (8)17: 159–163.

PROSSER, C. L., 1974, The species problem from the viewpoint of a physiologist. In MAYR, E., ed., *The species problem*. Arno Press, New York p. 339–369.

RADOMAN, P., 1953, Contribution à la connaissance des gastéropodes du Lac d'Ohrid (Macédoine). *Archiv of Biological Sciences (Beograd)*, 5: 55–59.

RENSCH, B., 1929, *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung.* Bornträger, Berlin, 206 p.

RENSCH, B., 1934, Süsswasser-Mollusken der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie Suppl.* 13 (Tropische Binnengewässer Bd. 5): 203–257.

RENSCH, B., 1936, *Die Geschichte des Sundabogens. Eine tiergeographische Untersuchung.* Bornträger, Berlin, 318 p.

RICHARDS, C. S., 1973a, Inherited variability in the course of the intestine in *Biomphalaria glabrata. Malacological Review*, 6: 133–138.

RICHARDS, C. S., 1973b, Genetics of *Biomphalaria glabrata* (Gastropoda: Planorbidae). *Malacological Review*, 6: 199–202.

ROSZKOWSKI, W., 1929, On the systematic position and the geographical distribution of the genus *Myxas. Annales Zoologici Musei Polonici Historiae Naturalis*, 8: 64–97.

SACHS, L., 1969, *Statistische Auswertungsmethoden.* Springer, Berlin, 2. Aufl., xxxii + 677 p.

SAY, T., 1817, *Nicholson's Encyclopedia,* 1st American edition.

SCHLEE, D., 1971, *Die Rekonstruktion der Phylogenese mit Hennig's Prinzip.* Kramer, Frankfurt, 62 p.

SCRUTTON, R. A., 1976, Fragmente der kontinentalen Lithosphäre. *Endeavour* (dtsch. Ausg.), 35: 99–103.

SCUDDER, G. G. E., 1974, Species concepts and speciation. *Canadian Journal of Zoology*, 52: 1121–1134.

SIMPSON, G. G., 1961, *Principles of animal taxonomy.* Columbia Univ. Press, New York, xii + 247 p.

SOKAL, R. R. & SNEATH, P. H. A., 1963, *Principles of numerical taxonomy.* Freeman, San Francisco, 359 p.

SONNEBORN, T. M., 1974, Breeding systems, reproductive methods, and species problems in Protozoa. In MAYR, E., ed., *The species problem.* Arno Press, New York, p. 155–324.

SONNEBORN, T. M. & DIPPELL, R. V., 1943, Sexual isolation, mating types, and sexual responses to diverse conditions in variety 4, *Paramecium aurelia. Biological Bulletin*, 85: 36–43.

SOOS, A., 1935, Morphologie and Histologie des Geschlechtsapparates der ungarischen *Planorbis*-Arten. *Allattani Közlemények (Budapest)*, 32: 21–46.

SPERLICH, D., 1973, Populationsgenetik. Grundlagen und experimentelle Ergebnisse. Fischer, Stuttgart, ix + 197 p.

STANDEN, O. D., 1949, Experimental schistosomiasis. The culture of the snail vectors *Planorbis boissyi* and *Bulinus truncatus. Annals of Tropical Medicine and Parasitology*, 43: 13–22.

STANKOVIČ, S., 1960, The Balkan Lake Ochrid and its living world. Junk, Den Haag, 357 p.

STARMÜHLNER, F., 1974, The freshwater gastropods of Ceylon. *Bulletin of the Fisheries Research Station, Sri Lanka*, 25: 97–181.

STAROBOGATOV, Y. I., 1958, The system and phylogeny of Planorbidae (Gastropoda Pulmo-

nata). *Bulletin of the Moscow Naturalists Society, Biological Department*, 63: 37–53.

STAROBOGATOV, Y. I., 1967, On the systematization of freshwater pulmonate molluscs. *Akademiia Nauk USSR Trudy Zoologičeskogo Instituta*, 42: 280–304.

STURANY, R., 1894, Zur Molluskenfauna der europäischen Türkei. *Annalen des k.k. naturhistorischen Hofmuseums Wien*, 9: 369–390.

THENIUS, E., 1977, *Meere and Länder im Wechsel der Zeiten.* Springer, Berlin, etc., x + 200 p.

THIENEMANN, A., 1950, *Verbreitungsgeschichte der Süsswassertierwelt Europas. Versuch einer historischen Tiergeographie der europäischen Binnengewässer.* Schweizerbart, Stuttgart, xvi + 809 p.

TIMES ATLAS OF THE WORLD, 1967, Comprehensive edition. London, 123 pl., 272 p.

WAGNER, A. J., 1931, Anatomische, biologische und systematische Beiträge zur Kenntnis der ungarischen Limnaeen. *Annales Historico-Naturales Musei Nationalis Hungarici*, 27: 71–157.

WALTER, H. J., 1962, Punctuation of the embryonic shell of Bulininae (Planorbidae) and its possible taxonomic-phylogenetic implications. *Malacologia*, 1: 115–137.

WESTERLUND, C. A., 1865, *Sveriges Land- och Sötvatten-Mollusker.* Gleerups, Lund, 146 p.

WESTERLUND, C. A., 1873, *Fauna molluscorum terrestrium et fluviatilium Sueciae, Norvegiae et Daniae. Sveriges, Norges och Danmarks Land- och Sötvatten-Mollusker. II. Sötvattenmollusker.* Stockholm, 651 p.

WESTERLUND, C. A., 1875, Malakologische Studien, Kritiken und Notizen. *Malakozoologische Blätter*, 22: 51–98.

WESTERLUND, C. A., 1883, Von der Vega-Expedition in Asien gesammelte Binnenmollusken. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 15: 48–59.

WESTERLUND, C. A., 1885, *Fauna der in der palaearctischen Region lebenden Binnenconchylien. 5. Succinidae, Auriculidae, Limnaeidae, Cyclostomidae & Hydrocenidae.* Hakan Ohlsson, Lund, 135 p., Reg. 1–12.

WRIGHT, C. A., 1963, The freshwater gastropod Mollusca of Angola. *Bulletin of the British Museum (Natural History) Zoology*, 10: 447–528.

YEN, T.-C., 1939, Die chinensischen Land- und Süsswasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 444: 1–233.

YEN, T. C., 1949, A new name for *Carinorbis* Yen. *Journal of Paleontology*, 23: 573.

ZILCH, A., 1960, Gastropoda Euthyneura. In SCHINDEWOLF, *Handbuch der Paläozoologie* 6, pt. 2: xii + 834 p.

APPENDIX.   Alphabetical List of Collecting Sites (short forms listed in the text)

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Abitibi R. (NMC 25150)	Canada: Ontario: A. River at Hwy. 579, appr. 27 km N of Cochrane; A. H. Clarke VII-1961	Clute	49.13N	81.00W
Alexandria	Egypt: Ezbet Belal 25 km S of Alex.; Demian III-1966	Alexandria	31.13N	29.55E
Ann Arbor	USA: Michigan. Woods-pool at Zeeb Rd., Te V-1974	Ann Arbor	42.18N	83.43W
Ansbach	Germany: Bavaria: Scheerweiher, 3 km W of Ansbach; H. Stocker I-1966	Ansbach	49.18N	10.36E
Baalbeck	Lebanon (collector and date not indicated)	Ba'albek	34.00N	36.12E
Bad Villach	see Villach			
Bahr-el-Houlé	Syria: running and standing waters near Bahr-el-Houlé (Lake Samachonitides); Bourguignat (no date)	?		
Bangalore	India: Bangalore; Muraleedharan, XII-1973 Mandahl-Barth dedit	Bangalore	12.58N	77.35E
Barracuta (L.)	Australia: East Victoria; Neboiss I-1975	?		

APPENDIX.   Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Benambra	Australia: Corryong Rd., 8 km N of B.; in water beside road; Dartmouth Survey X-1973	Corryong	36.11S	147.58E
Bharatpur	India: Bird sanctuary near Bh.; D. Haas I-1974	Bharatpur	27.14N	77.28E
Biwa (L.)	Japan: Lake Biwa; at Shiotsu and Oura: T. Miura VI-1975; at Eizan: H. D. Boeters II-1975	Kinomoto Otsu	35.33N 35.00N	136.12E 135.50E
Bodensee	Germany: Lake of Constance at Sipplingen/Überlingen; Meier-Br. IX-1961	Überlingen	47.46N	9.10E
Bombala (NMV 2305)	Australia: New S Wales: Saucy Ck.; 10 km S of B., on Cann Valley Hwy.; A.B.R.S. Snail Survey IV-1975	Bombala	36.55S	149.16E
Bukateja	S-central Java; Tjhen VI-1976	Purbolinggo	7.22S	109.15E
Cairo	Egypt: Drain in Giza near pyramids; Demian X-1974	Giza Pyram.	29.59N	31.07E
Chongpyong	Rep. of Korea: Kyong-gi-do: fish pond; Meier-Brook VI/XII-1970	Kapyong	37.53N	127.30E
Diyarbakir	Turkey: Vilayet Diyarbakir; Paydak VI-1972; H. Schütt dedit	Diyarbakir	37.55N	40.14E
Dobersdorfer See	N Germany: Holstein: Probsteierhagen; Meier-Brook IX-1960	Schönberg	54.24N	10.23E
Drusenheim	France: Bas Rhin; Meier-Brook III-1961	Drusenheim	48.46N	7.58E
Dudinska	U.S.S.R.: Siberia: Dudinka/Yenisey, Swed. Sib. Exped. VII-1876	Dudinka	69.27N	86.13E
Ettenheim	SW Germany: Baden; fishpond; Meier-Brook VI-1961	Ettenheim	48.16N	7.52E
Fehmarn	see Wallnau			
Fischau	Austria: Therme Bad Fischau; Meier-Br. IX-1968; Jungbluth X-1974	Bad Fischau	47.50N	16.11E
Gawargin	Afghanistan: Prov. of Helmand (31.26N 64.20E), alt. "750 m" (according to Times Atlas, coordinates are between 200 and 500 m in alt.!); Kawata IX-1968; Mandahl-Barth dedit	Zaras	31.18N	64.13E
Greifensee	Switzerland: E of Zürich; Meier-Brook VII-1961	Greifensee	47.18N	8.42E
Haarlem	Netherlands: "Lake" in Kennemerduinen; R. Bank VIII-1977	Haarlem	52.23N	4.38E
Hanechi-son (ANSP A288)	Japan: Okinawa: channel and ditch along rt. 124 betw. Maeshine and Gabusoka; Davis III-1968	Nakaoshi	26.43N	127.57E

APPENDIX.   Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Haslacher See	Germany: Bavaria: near Burggen; Meier-Brook VIII-1959	Schongau Lech	47.49N	10.54E
Hong Kong	Hong Kong: Island peak in mountain stream; A. J. Brandt IV-1974	Victoria	22.16N	114.13E
Iceland, SE	A. Skaftaffellssysla; pond on Stapasandur, nr. Thveit; Einarsson VIII-1976; dedit Sigurdsson	Bjarnarnes	64.19N	15.13W
Iceland, S	Arnessysla: Opnur, Stora-saurbae, Ölfus; Sigurdsson VII-1976	Kaldadarnes	63.56N	21.10W
Iceland, W	Snaefellsnessysla: Stadarsveit, Kúka & Hofgardatjörn, Yovi-Gardar; Sigurdsson VII-1976	Stadastadur	64.49N	23.00W
Inner Mongolia	See Läger XI			
Iran, S	locality? III-1975 Massoud dedit	?		
Kaejong	Rep. of Korea: Cholla-puk-do; ditch W of rd. Iri-Kunsan; Meier-Brook IX-1970	Kunsan	35.57N	126.42E
Karabella	U.S.S.R.: Kola Peninsula; on Ribatski; Sandebergs Exped. VII-1877	?		
Kasseeteich	Germany: Holstein: near Probsteierhagen; Meier-Brook III-1960	Kiel	54.20N	10.08E
Kolksee	N Germany: Holstein: forest lake near rd. Preetz-Plön; Meier-Br. VII-74	Preetz	54.14N	10.17E
Krasnojarsk (NHRMS 404)	U.S.S.R.: Siberia; Swed. Sib. Exped. 1876	Karsnojarsk	56.05N	92.46E
Kuala Lumpur	Malaysia: 5 km from K.L., large unused tin-mining pool. On grass and *Eichhornia*. J. K. Lie VI-1973	Kuala Lumpur	3.08N	101.42E
Kuehren	N Germany: Holstein: Kührener Viehteich; Meier-Brook VIII-1974	Preetz	54.14N	10.17E
Kumluca	Turkey: well NE Kumluca; Kinzelbach VIII-1975	Kumluca	36.23N	30.17E
Kunsan	Rep. of Korea: Cholla-puk-do: reservoir betw. K. and Air base; Meier-Brook VIII-1970	Kunsan	35.57N	126.42E
Kwekerslaan	Netherlands: greenhouses in Kw., Haarlem; R. Bank VII-1977	Haarlem	52.23N	4.38E
Lake . . .	see proper name			
Läger XI (NHRMS 2198)	P. R. China: Inner Mongolia: Honnentjaggan-tschollogol, a northern tributary of Hoang-ho; Sven Hedin Exped.; Hummel VIII-1927	(?) Ch'ing-tai	41.46N	113.29E
Lesser Slave Lake (NMC 29922)	Canada: Alberta: Slave Lake; Athearn; VII-1965 A. H. Clarke id. et dedit	(?) Slave Lake	55.17N	114.43W

APPENDIX.   Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Liberia	Centra Liberia; Höfler et Knüttgen V-1974	?		
Limyra	Turkey: mouth of a creek 5 km E of Limyra near Finike; Kinzelbach VIII-1975	Finike	36.18N	30.08E
Mainz	W Germany: pond in Bot. Garden Mainz Univ.; Kinzelbach 1973–1974	Mainz	50.00N	8.16E
Malacca	Malaysia: 20 km inland from M., stream running through paddy-field; J. B. Sigurdsson II-1977	Malacca	2.14N	102.14E
Mauna-gawa	Japan: Okinawa; branch of Mauna-gawa, E of Teguchi-village; Davis III-1968	Toguchi	26.40N	127.53E
Mauritius	Beau Bassin, canal; C. N. Courtois VI-1973	Rose Hill	20.14S	57.27E
Merauke (RMNH 5322)	West Irian (New Guinea): pool N of M. in swampy area (cf. v. Benth.-J., 1963: 494); Holthuis III-1955	Merauke	8.30S	140.22E
Mindanao (NHRMS 4166)	Philippines: Davao Penal Colony, 40 km N of Davao City, creek; B. Hubendick VII-1952	Davao	7.05N	125.38E
Motobu-cho (ANSP A266)	Japan: Okinawa: E of Teguchi-village Davis III-1968	Tohuchi	26.40N	127.53E
Niederzell/Unter-see	Germany: Lake of Constance: Island of Reichenau (also called Unterzell)	Radolfzell	47.44N	8.59E
Ohrid (L.)	Yugoslavia: Macedonia: Lake Ohrid near Sveti Zaum; Rähle VI-1973	Ohrid	41.06N	20.49E
Onna-son (ANSP A 453)	Japan: Okinawa: paddy field W of Atsuta, along Rt. 1; Davis IV-1968	Atsuta	26.30N	127.50E
Paratunka (NHRMS 3727)	U.S.S.R.: Kamchatka: hot springs near P.; Hultén II-1921	Paratunka	52.58N	158.14E
Pleistinger Wörth	S Germany: Bavaria: island in Donau; Hässlein VIII-1965	Vilshofen	48.38N	13.12E
Prespa (L.)	Yugoslavia: Macedonia: Lake Prespa, Rähle VI-1973; Maassen V-1976	Resen	41.05N	21.01E
Ragunda (NHMG 11249)	Sweden: Jmt.: SW Stormoberget, Ammeråns N strand; Waldén et Wanntorp VII-1961	Ragunda	63.06N	16.25E
Rasno-volok (NHRMS 347)	U.S.S.R.: Kola-peninsula; turbid marsh; Sandebergs Exped. VII-1877	?		
Rhine River Backwater	Germany: Baden: Plittersdorf; Meier-Brook III-1961	Rastatt	48.51N	8.13E

APPENDIX.   Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° '	Long. ° '
St. Point (Lac)	France: Dép. Jura: Lac de St. Point F. Geissert 1959	St. Point	46.49N	6.17E
Samava	Iraq: As Samawah/Euphrates; Schlaefli 1873	As Samawah	31.18N	45.18E
Sashiki-son (ANSP A374)	Japan: Okinawa; ditch in Fusozaki along Kaneku-ko Bay; Davis III-1968	Baten	26.12N	127.46E
Sayedabad	"Afghanistan" (30.49N 67.51E); (according to Times Atlas, 1967, these coordinates are in West Pakistan, Quetta Prov.), alt. 2500 m; Kawata VIII-1968; Mandahl-Barth dedit	?Hindubagh	30.51N	67.50E
Selenter See	Germany: Holstein; Meier-Br. III-1960	Lütjenburg	54.17N	10.36E
Seychelles (IRSNB I.G. 25.536)	Ile de Mahé, Riv. Sèche (Route de Misère), Sta. 40; G. Marlier X-1976	Mahé I.	4.41S	55.30E
Siggen	S Germany: Allgäu: Krs. Wangen; Neuweiher near Siggen; Meier-Brook IV-1974	Isny	47.42N	10.02E
Sjaelland	Denmark: lake 1 km N of Jorløse, E of rd. Kalundborg-Slagelse; Burgemeister VII-1976	Jerslev	55.37N	11.15E
Soufflenheim	France: Bas Rhin; inundated meadow NE rd. S Sessenheim; Meier-Brook V-1963	Soufflenheim	48.50N	7.57E
Speyer	SW Germany: Autobahnsee NE Speyer; Fischenich III-1974; Kinzelbach ded.	Speyer	49.18N	8.26E
Stuttgart	Germany: Württemberg: forest pool near Stuttgart-Büsnau; Meier-Brook V-1977	Stuttgart	48.47N	9.12E
Tärna	Sweden: Ly Lpm., SE Granås; 500 m SE of Granås; H. Waldén, Svensson, and Wanntorp VIII-1962	?		
Tage (L.) (RMNH alc. 4985)	West Irian (New Guinea): Lake Tage, near missionary post Tage, Wissel Lake region (cf. v. Benth.-J., 1963: 497); L. D. Brongersma XII-1954	between Uwapa and Mbambawa	3.46S 3.42S	135.31E 137.31E
Taiwan	Rice fields near Hualien-Airport; Lo VI-1975	Hualien	23.58N	121.53E
Tasik Madu	N Bali: Lovina-beach; Tjhen VI-1976	Singaradja	8.06S	115.07E
Thailand (SMF 193798)	Bangkok: Zoolog. Garden; R. Brandt VI-1965	Bangkok	13.44N	100.30E

APPENDIX.   Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Thailand (SMF 197350)	Klong Killard, 4.7 km from Grabi to Khao Thong; R. Brandt X-1969	Krabi	8.04N	98.52E
Titisee	Germany: Baden: Schwarzwald; Meier-Brook X-1961	Titisee	47.55N	8.10E
Tomigusukuson (ANSP A416)	Japan: Okinawa; ditch near Iraha, 1.6 km S Naha air base; Davis III-1968	Oroku/Naha	26.10N	127.40E
Tondano (ZMA)	Sulawesi (Celebes): River near Tondano; Siboga Expedition	Tondano	1.19N	125.56E
Tübingen	S Germany: Quarry pool near Wendelsheim, 6 km W of T.; Meier-Brook VI-1973	Tübingen	48.32N	9.04E
Tulom River (NHRMS 350)	U.S.S.R: Kola peninsula: Tulom R. 10 to 20 verst from Kola; Sandebergs Exped. VII-1877	Kola	68.53N	33.01E
Untersee	see Niederzell			
Ursee	SW Germany: bog in Schwarzwald between Feldberg and Lenzkirch; Meier-Brook IV/VIII-1963	Lenzkirch	47.52N	8.13E
Valtjärn (NHMG 66-11.853)	Sweden: Jmt, 1300 m N of Mattmar K:a, creek just W of Valtjärn; Waldén IX-1966	Mattmar	63.19N	13.45E
Vikarsjön (NHMG 64-11490)	Sweden: Hrj, Vikarsjön S. str. v. Kvarnåns utfl.; Waldén, Svensson and Wanntorp VIII-1962	?		
Villach	Austria: Kärnten: Therme Bad Villach; Mildner VIII-1974	Villach	46.37N	13.51E
Vojmån (NHMG 67-11.982)	Sweden: Ås Lpm, northern part of Gotajaure; Waldén and Hultin VIII-1968	?		
Wallnau/Fehmarn	Germany: Holstein: Island of Fehmarn; Meier-Brook III-1960	Orth	54.27N	11.04E
Westensee	Germany: Schleswig; J. Rentner V-1961	Flemhude	54.20N	9.58E
Windgfällweiher	SW Germany: tarn in Schwarzwald between Feldberg a. Lenzkirch; Meier-Brook VI/IX-1964	Lenzkirch	47.52N	8.13E
Wollmatingen	S Germany: Wollmatinger Ried, part of Bodensee near Reichenau; Meier-Brook VI-1961	Konstanz	47.40N	9.10E
Zürichsee	Switzerland; J. Walter IV-1974	Zürich	47.23N	8.33E